Vol. LIV No. 2

THE BOTANICAL GAZETTE

August 1912

Editor: JOHN M. COULTER

CONTENTS

Spermatogenesis in Equisetum — Lester W. Sharp

The Primary Color-Factors of Lychnis and Color-Inhibitors of Papaver Rhoeas — George Harrison Shull

Contributions from the Rocky Mountain Herbarium. XI — Aven Nelson

Beneficial Effect of Creatinine and Creatine on Growth — J. J. Skinner

Briefer Articles

A Note on the Generations of Polysiphonia — George B. Rigg and Annie D. Dalgity

Current Literature

The University of Chicago Press
CHICAGO, ILLINOIS

Agents
THE CAMBRIDGE UNIVERSITY PRESS, *London and Edinburgh*
WILLIAM WESLEY & SON, *London*
TH. STAUFFER, *Leipzig*
THE MARUZEN-KABUSHIKI-KAISHA, *Tokyo, Osaka, Kyoto*

The Botanical Gazette

A Monthly Journal Embracing all Departments of Botanical Science

Edited by JOHN M. COULTER, with the assistance of other members of the botanical staff of the University of Chicago.

Issued August 16, 1912

Vol. LIV CONTENTS FOR AUGUST 1912 No. 2

SPERMATOGENESIS IN EQUISETUM. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 158 (WITH PLATES VII AND VIII). *Lester W. Sharp* - - - - - - - - - 89

THE PRIMARY COLOR-FACTORS OF LYCHNIS AND COLOR-INHIBITORS OF PAPAVER RHOEAS. *George Harrison Shull* - - - - - - - - - - - - - 120

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. XI (WITH TWO FIGURES). *Aven Nelson* - - - - - - - - - - - - - - - - - 136

BENEFICIAL EFFECT OF CREATININE AND CREATINE ON GROWTH (WITH ONE FIGURE). *J. J. Skinner* - - - - - - - - - - - - - - - - 152

BRIEFER ARTICLES

A NOTE ON THE GENERATIONS OF POLYSIPHONIA (WITH ONE FIGURE). *George B. Rigg* and *Annie D. Dalgity* - - - - - - - - - - - - - - - - - 164

CURRENT LITERATURE

BOOK REVIEWS - 166

FOREST PHYSIOGRAPHY. A YOSEMITE FLORA

NOTES FOR STUDENTS - - - - - - - - - - - - - - - - - - 168

The Botanical Gazette is published monthly. ¶The subscription price is $7.00 per year; the price of single copies is 75 cents. ¶Postage is prepaid by the publishers on all orders from the United States, Mexico, Cuba, Porto Rico, Panama Canal Zone, Republic of Panama, Hawaiian Islands, Philippine Islands, Guam, Tutuila (Samoa), Shanghai. ¶Postage is charged extra as follows: For Canada, 35 cents on annual subscriptions (total $7.35), on single copies, 3 cents (total 78 cents); for all other countries in the Postal Union, 84 cents on annual subscriptions (total $7.84), on single copies, 11 cents (total 86 cents). ¶Remittances should be made payable to The University of Chicago Press, and should be in Chicago or New York exchange, postal or express money order. If local check is used, 10 cents must be added for collection.

The following agents have been appointed and are authorized to quote the prices indicated:

For the British Empire: The Cambridge University Press, Fetter Lane, London, E.C., and William Wesley & Son, 28 Essex Street, Strand, London. Yearly subscriptions, including postage, £1 12*s.* 6*d.* each; single copies, including postage, 3*s.* 6*d.* each.

For the Continent of Europe: Th. Stauffer, Universitätsstrasse 26, Leipzig, Germany. Yearly subscriptions, including postage, M. 33 each; single copies, including postage, M. 3.60 each.

For Japan and Korea: The Maruzen-Kabushiki-Kaisha, 11 to 16 Nihonbashi Tori Sanchome, Tokyo, Japan. Yearly subscriptions, including postage, Yen 15.75 each; single copies, including postage, Yen 1.75 each.

Claims for missing numbers should be made within the month following the regular month of publication. The publishers expect to supply missing numbers free only when they have been lost in transit.

Business correspondence should be addressed to The University of Chicago Press, Chicago, Ill.

Communications for the editor should be addressed to him at The University of Chicago, Chicago, Ill.

Contributors are requested to write scientific and proper names with particular care, to use the metric system of weights and measures, and in citations to follow the form shown in the pages of the BOTANICAL GAZETTE.

Papers in excess of thirty-two printed pages are not accepted unless the author is willing to pay the cost of the additional pages, in which case the number of pages in the volume is correspondingly increased.

Illustrations are furnished without cost to author only when suitable originals are supplied. A copy of the suggestions made in the January number, 1907, will be sent on application. It is advisable to confer with the editors as to illustrations required in any article to be offered.

Separates, if desired, must be ordered in advance of publication. Twenty-five separates of original articles without covers will be supplied gratis. A table showing approximate cost of additional separates is printed on an order blank which accompanies the proof; a copy will be sent on request.

Entered August 21, 1896, at the Post-office at Chicago, as second-class matter, under Act of Congress March 3, 1879.

VOLUME LIV NUMBER 2

THE

BOTANICAL GAZETTE

AUGUST 1912

SPERMATOGENESIS IN EQUISETUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 158

LESTER W. SHARP

(WITH PLATES VII AND VIII)

Historical résumé

The cilia-bearing organs of the motile cells of plants have formed the basis of a number of researches during recent years. In the majority of cases in which the bearing of the results has been given consideration, the discussion has centered about the morphological nature of these organs, and in this discussion a very prominent place has been taken by the centrosome.

Among the earliest investigations in this field were those of STRASBURGER (**78**) on the algae. During the development of the swarm spores of *Oedogonium*, *Cladophora*, and *Vaucheria* he found that the nucleus approaches the plasma membrane, which at that point becomes thickened, forming a lens-shaped *Mundstelle*. From this grow out the cilia, and at the base of each a small refractive granule is present. A full discussion of the morphological nature of these cilia-bearing structures and an extensive comparison with those of higher plants were given in connection with a later work (**80**). The main point to be noted at this time is that STRASBURGER believed that the blepharoplasts of higher plants have been derived from such swollen *Hautschicht* organs in the algae, and that all of them are morphologically distinct from centrosomes.

DANGEARD (**17**) found a deeply staining granule at the base of the cilia in *Chlorogonium*, but did not consider it a centrosome. In

a later paper (**18**) he states that in *Polytoma* the cilia are inserted on a similar granule which is believed to be a swelling of the ectoplasm. In some cases he saw a delicate filament connecting this with another minute body at the surface of the nucleus.

In *Hydrodictyon* (TIMBERLAKE **85**) the cilia are inserted on a small body lying in contact with the plasma membrane, but independent of the latter. Protoplasmic strands join this structure with the nucleus. At the poles of the spindle during the differentiation of the spore *Anlage*, and later near the nucleus, two heavily staining granules were seen, but their origin and further history were not worked out.

In the zoospore origin of *Derbesia*, according to DAVIS (**21**), the nucleus migrates toward the cell membrane and from it many granules, which are not centrosomes, move out along radiating strands of cytoplasm to the surface of the cell, where by fusion they form a ring-shaped structure from which the cilia develop.

The development of the spermatozoid in *Chara* has been described by BELAJEFF (**2**) and by MOTTIER (**71**). Here the blepharoplast arises as a differentiation of the plasma membrane and bears two cilia. No centrosomes or *Plasmahöcker* were observed at the base of the cilia, although SCHOTTLÄNDER (**75**) had previously reported centrosomes in the cells of the spermatogenous filament.

GRIGGS (**34**) describes in a recent paper a deeply staining body at the insertion point of the cilia in the zoospore of the fungus *Rhodochytrium*. This is connected by fine cytoplasmic fibers with the nucleus. The author states that no centrosomes were observed.

In the myxomycete *Stemonitis* JAHN (**56**) has made a highly suggestive observation. During the last mitosis in the formation of the swarmers the spindle poles are occupied by centrosomes. During the anaphases the flagella of the two resulting swarmers are seen growing out directly from these centrosomes.

Among the bryophytes the blepharoplasts in *Marchantia* and *Fegatella* have received the most attention. According to IKENO (**53**) a centrosome comes out of the nucleus at each spermatogenous division in *Marchantia* and divides to two, which diverge to opposite

sides of the cell, occupy the spindle poles, and disappear at the close of mitosis. It is possible that they are included within the membranes of the daughter nuclei. After the last (diagonal) division, however, they remain in the cytoplasm as the blepharoplasts, elongating and bearing two cilia. IKENO regards these bodies as true centrosomes. He further believes that the blepharoplasts of pteridophytes and gymnosperms are derived ontogenetically or phylogenetically from centrosomes, but that all bodies called centrosomes in plants may not be homologous. In a paper appearing two years later, MIYAKE (**66**) states that although an inconstant aster, often with a dot at the focus, may appear in the spermatogenous divisions, no body like IKENO's centrosome is present, except at the last mitosis, when a body lies at each spindle pole as figured by that author. Essentially the same results were obtained in *Fegatella*, *Pellia*, *Aneura*, and *Makinoa*. MIYAKE believes that the centrosome hitherto reported in the cells of the Hepaticae is nothing but a center of cytoplasmic radiation, and inclines toward the view of STRASBURGER that the blepharoplast and the centrosome are not homologous structures. ESCOYEZ (**22**) states that in *Marchantia* and *Fegatella* two "corpuscles" appear in the spermatid mother cell in contact with the plasma membrane. These occupy the spindle poles and in the spermatids function as blepharoplasts. ESCOYEZ regards these organs as distinct from centrosomes, though their origin was not traced. Centrosomes are reported by SCHAFFNER (**74**) in all the spermatogenous divisions in *Marchantia*. After the last mitosis these behave as blepharoplasts, which are consequently looked upon as modified centrosomes. BOLLETER (**8**) found in *Fegatella* a centrosome-like body near the spindle pole at the last division and observed its nuclear origin. He believes that it is present in the earlier division also.

In the antheridium of *Riccia* LEWIS (**61**) reports centrosome-like structures in the early and diagonal divisions. These apparently arise *de novo* in the cytoplasm at each mitosis, showing no continuity through the succeeding cell generations except at the last mitosis, when they persist and become the blepharoplasts. LEWIS does not think these bodies represent centrosomes.

The most recent investigations of the blepharoplast in bryo-

phytes are embodied in two papers appearing in 1911. In the first of these WOODBURN (**95**) gives an account of spermatogenesis in *Porella*, *Asterella*, *Marchantia*, and *Fegatella*. He finds that the blepharoplast is first distinguishable as a spherical granule in the cytoplasm of the spermatid, and holds that it represents, as MOTTIER (**71**) had formerly suggested, an individualized part of the kinoplasm arising *de novo* in certain spermatogenous cells. WILSON (**93**) describes the phenomena occurring in *Pellia*, *Atrichum*, and *Mnium*. In *Mnium* and *Atrichum* the spermatogenous divisions show no centrosomes, while in *Pellia* centrospheres, and probably centrosomes, are present during the later mitoses. The origin of the blepharoplast as here described is very peculiar. In the spermatid of *Mnium* a number of bodies separate from the nucleolus and pass out into the cytoplasm where they coalesce to form a "limosphere." The nucleolus then divides into two masses, both of which pass into the cytoplasm; one functions as the blepharoplast while the other gives rise to an accessory body. In *Atrichum* the first body separated from the nucleolus becomes the blepharoplast, a second forms the limosphere, and a third the accessory body. In *Pellia* the origin of these structures was not determined. In all three plants the blepharoplast goes to the periphery of the cell and produces a threadlike structure along the plasma membrane. The nucleus then moves against this thread and the two metamorphose together to form the spermatozoid. WILSON regards the blepharoplast as "probably derived from a centrosome."

According to HUMPHREY (**49**) the blepharoplast of *Fossombronia* is first seen in the cytoplasm of the spermatid.

The early papers dealing with the spermatozoid in pteridophytes, such as those of BUCHTIEN (**9**), CAMPBELL (**12**), BELAJEFF (**1**), GUIGNARD (**35**), and SCHOTTLÄNDER (**75**), give us little or no information concerning the development of the blepharoplast. Our more definite knowledge of this subject dates from 1897, when BELAJEFF published three short papers. In the first of these (**3**) it is stated that the fern spermatozoid consists of a thread-shaped nucleus and a plasma band, with a great many cilia growing out from the latter. In the plasma band is inclosed a thin thread which arises by the lengthening of a small body seen in the sperma-

togenous cell. In the second paper (**4**) the blepharoplast of *Equisetum* is first described as a crescent-shaped body lying against the nucleus of the spermatid. This body stretches out to form the cilia-bearing thread. The third contribution (**5**) is a short account of the metamorphosis of the spermatid in *Chara*, ferns, and *Equisetum*. In all of these forms a small body elongates to form a thread upon which small *Höcker* arise and grow out into cilia. In a comparison with animal spermatogenesis, BELAJEFF here homologizes the *Körperchen* (blepharoplast) in the spermatid, the thread to which it elongates, and the cilia of the plant, with the centrosome, middle piece, and tail (perhaps only the axial filament), respectively, of the animal. The following year, in connection with a further discussion, he figured the details as made out by him in *Gymnogramme* and *Equisetum* (**6**). In *Gymnogramme* the blepharoplasts appear at opposite sides of the nucleus in the spermatid mother cell, while in *Equisetum* a single blepharoplast is first figured lying close to the nucleus of the spermatid, behaving as outlined in the earlier accounts.

One of the most interesting cases is that of *Marsilia*, first described by SHAW (**76**). According to this investigator a small granule or "blepharoplastoid" appears near each daughter nucleus of the mitosis which differentiates the grandmother cell of the spermatid. During the next division these divide but soon disappear, and a blepharoplast appears near each spindle pole. In the next cell generation (spermatid mother cell) the blepharoplast divides to two which become situated at the spindle poles in the final mitosis. In the spermatid the blepharoplast shows a small internal granule; this multiplies to several and forms a band which elongates spirally with the nucleus and bears the cilia. SHAW sees in these facts no ground for the homology of the blepharoplast and the centrosome. BELAJEFF'S paper dealing with *Marsilia* appeared in the following year (**7**). He found that centrosomes occur at the poles during all, excepting possibly the first, of the series of divisions which result finally in the 16 spermatids. After each mitosis the centrosome divides to two which occupy the poles during the next mitosis, and in the spermatid it performs the function of a blepharoplast. BELAJEFF regards this as a strong confirmation

of his theory that the blepharoplast and the centrosome are homologous structures.

In *Adiantum* and *Aspidium* (THOM **84**) the blepharoplast is described as a round body in the cytoplasm of the spermatid. It is stated that it does not act as a centrosome during division, though no figures of these stages are shown.

The most recent work dealing with the blepharoplast in pteridophytes is that of YAMANOUCHI (**97**) on *Nephrodium*. In this form there are no centrosomes in the whole life history. The two blepharoplasts, which arise *de novo* in the cytoplasm of the spermatid mother cell, take no active part in nuclear division, merely lying near the poles of the spindle. In the spermatid the blepharoplast elongates in close union with the nucleus to form the cilia-bearing band.

The first known blepharoplast in plants above the algae was discovered in *Ginkgo* by HIRASÉ (**45**) in 1894. He observed two, one on either side of the body cell nucleus, and because of their great similarity to certain structures in animal cells believed them to be attraction spheres. It was not until two years later that this investigator announced the discovery of the swimming sperm of *Ginkgo*. In 1897 WEBBER (**89**) observed the same structures, noting their cytoplasmic origin. On account of several differences existing between these bodies and known centrosomes he expressed the belief that they are not true centrosomes, but distinct organs of spermatic cells, and first applied to them the name blepharoplast. FUJII (**30, 31, 32**) gave several figures of spermatogenesis in *Ginkgo*, which agree with the accounts of HIRASÉ and WEBBER. The same subject has been dealt with more recently by MIYAKE (**67**).

In two short papers appearing in 1897, WEBBER described the blepharoplast of *Zamia* (**87, 88**), and in 1901 a very full account was published (**90**). According to this author two blepharoplasts arise *de novo* in the cytoplasm. They are surrounded by radiations up to the time of the division of the body cell, but these have no part in the formation of the spindle, which is entirely intranuclear. During mitosis the blepharoplasts, lying opposite the poles, become vacuolate and break up to many granules which unite to form the

cilia-bearing band. In this paper WEBBER gives a very extensive discussion of the morphological nature of the blepharoplast which will be referred to later.

IKENO (**51**) expressed the opinion that the blepharoplast of *Ginkgo* and the cycads is not only similar to a centrosome but is a true centrosome, a view shared by GUIGNARD (**36**). Soon after this IKENO's full account of gametogenesis and fertilization in *Cycas* appeared (**52**). In this paper it was shown that the blepharoplasts appear in the body cell, lie opposite the spindle poles during mitosis, and break up to granules which fuse to form the spiral band in a manner similar to that described by WEBBER for *Zamia*.

Several years later the same writer published two papers dealing with the morphological nature of the blepharoplast. In the first of these (**54**) he reviews the former work on the subject and makes comparisons with analogous phenomena in animals, which he believes sustain the homologies of BELAJEFF. He points out that in *Marchantia* centrosomes are present in all the spermatogenous divisions, while in other liverworts they appear much later, and from this argues that the bryophytes show various stages in the elimination of the centrosome. He strongly reasserts his belief that blepharoplasts are centrosomes and speaks of the "Umwandlung eines Zentrosoms zu einem Blepharoplast" in the development of a spermatid into a spermatozoid. The *Hautschicht* organs of the algae are also held to be ontogenetically or phylogenetically derived from centrosomes. In the later contribution (**55**) he insists less strongly upon the morphological identity of all blepharoplasts, separating them into three categories: (1) centrosomatic blepharoplasts, including those of the myxomycetes, bryophytes, pteridophytes, and gymnosperms; (2) plasmodermal blepharoplasts, those of *Chara* and some Chlorophyceae; (3) nuclear blepharoplasts, found only in a few flagellates.

The blepharoplasts of *Microcycas* (CALDWELL **11**) appear in the cytoplasm of the body cell, often very close to each other. They are surrounded by prominent radiations and lie opposite the spindle poles through mitosis. At metaphase they have already broken up and begun the formation of the spiral band.

CHAMBERLAIN (**15**) observed in the cytoplasm of the body cell

of *Dioon* a number of very minute "black granules" which he was inclined to believe originate within the nucleus. Very soon two undoubted blepharoplasts are present, and are apparently formed by the enlargement of two of the original black granules. Very conspicuous radiations develop about them, and after mitosis they form the cilia-bearing band as in other cycads. In an earlier paper (**13**) on the homology of the blepharoplast CHAMBERLAIN expressed the opinion that it is to be regarded as a centrosome.

From the foregoing historical review it is evident that there are two general views concerning the morphological nature of the blepharoplast as seen in bryophytes, pteridophytes, and gymnosperms:

(1) The blepharoplast represents a centrosome (HIRASÉ, IKENO, BELAJEFF, GUIGNARD, SCHAFFNER, WILSON, CHAMBERLAIN).

(2) The blepharoplast is specialized kinoplasmic or cytoplasmic material but not a centrosome (STRASBURGER, WEBBER, SHAW, LEWIS, THOM, ESCOYEZ, WOODBURN).

The present study of spermatogenesis in *Equisetum* was undertaken in the hope of shedding further light upon the relative merits of these two views, and it is with particular reference to this problem that the results are given consideration in the following pages.

Materials and methods

Spores were collected in Chicago, May 15, 1911, and sown upon clean sand watered from below. These cultures were kept under ground glass in the greenhouse of the Hull Botanical Laboratory. In five weeks, a somewhat longer time than is usually necessary, sperms were swimming in large numbers.

Several killing fluids and stains were used. By far the most satisfactory results were obtained with the iron-hematoxylin of Haidenhain after a killing fluid made up as follows: bichromate of potash 2.5 gm., bichloride of mercury 5 gm., water 90 cc., freshly distilled neutral formalin 10 cc.

Description

The usual statement concerning the antheridium of *Equisetum* is that it occurs in two forms, developing in some cases like the antheridium of the eusporangiate pteridophytes, and in others from a

papillate cell as in the Filicales. The mode of development has usually been correlated with the position of the antheridium initial in the prothallium. An adequate study of antheridium development was not made in connection with the present work on *Equisetum arvense*, but of the many young antheridia examined not one was unmistakably of the latter form. Apparently any of the cells of the prothallium, especially those near the apex, are able to divide periclinally and produce antheridia of the well known imbedded type.

In the nuclei of the spermatogenous cells the chromatin has the form of a ragged network of rather close mesh, the greater part of it being accumulated in knots at the intersections. One or more conspicuous nucleoli are present. The cytoplasm during the earlier cell generations may contain many plastids in various stages of disorganization; in most cases these are no longer evident by the time the 8 or 16-celled stage has been reached, but occasionally they persist and are found in considerable numbers in the penultimate cell generation, or even in the spermatids. It is obviously necessary to select for critical study of the details of blepharoplast development those antheridia in which the plastids do not introduce an element of uncertainty.

The main point to be noted in connection with mitosis in the early cell generations is that there are present no bodies which could possibly be interpreted as centrosomes. The spindle fibers are very weakly developed and end at the poles without any signs of centrosomes, centrospheres, or asters.

The first conspicuous indication of approaching sperm formation is seen in the rounding off of the cells of the penultimate generation (fig. 1). They begin to separate at the corners and gradually draw away from each other until they are entirely free. Although the division of these cells results in the production of sperms n pairs, it becomes inaccurate to speak here of mother cells with two sperms developing in each, since the intervening walls may persist until the sperms are mature or may break down at once. By designating them "penultimate cells" this ambiguity is avoided. Their number at the time of rounding off varies greatly in different antheridia. The observed range was 64 to 512, which means that

the number of sperms per antheridium varies from 128 to 1024 (approximately). Correlated with this is a great difference in the size of the antheridia. The sperms themselves also show considerable variation in dimension, as a comparison of figs. 28 and 29 will show. The nucleus of the penultimate cell at the time of separation is in the resting condition. The cytoplasm has a very fine and uniform structure, and in most cases is entirely free from plastids or other inclusions. Vacuoles are present only very rarely.

While the penultimate cells are rounding off from one another there appears in the cytoplasm near the nucleus a very minute granule which stains intensely with iron-hematoxylin (fig. 2). Its diameter lies between 0.25 and 0.3 μ. Very faint cytoplasmic radiations extend out from it in all directions, forming a very weakly developed aster. In other cells of the same antheridium the granule is seen to be dumb-bell shaped, and in still other cells distinctly double, showing that it divides to two (figs. 3, 4). These paired bodies are the blepharoplasts. Immediately after division their diameter increases to 0.5 μ. Their radiations become more pronounced and the nucleus often becomes flattened or slightly indented at the point where they lie, as in fig. 8.

The origin of the single granule cannot be stated with certainty. When first made out it holds a position near the nuclear membrane, a fact which would suggest its nuclear origin, but no other evidence in favor of this interpretation was obtained. The nuclear membrane shows no indication of recent disturbance. Moreover, it is highly improbable that such a granule could be distinguished within the nucleus because of its small size, its similarity in staining reaction to the chromatin network, and the density of the latter. Some light may be shed upon the question by exceptional cells like that shown in fig. 5. Here are scattered through the cytoplasm many very small intensely staining bodies, a few of which occur in pairs. When first seen these granules lie in all positions with respect to the nucleus and the plasma membrane. Some of the paired granules are distinctly larger than the single ones; the pair nearest the nuclear membrane is always the largest, has the most evident radiations, and is without doubt the same structure shown in fig. 4.

In other cells of the same antheridium only this pair is present, the other bodies, if formerly present, having been resorbed.

One can hardly speak conclusively regarding all points in the history of such minute structures. The evidence at hand, however, inclines the present writer toward the belief that the original single granule, which by division gives rise to the two blepharoplasts, is in some cases one of a number which may appear *de novo* in the cytoplasm and start development.

The two blepharoplasts, which lie very close together for a little time immediately following their formation from a single body, soon begin to move apart. As they do so a very distinct central spindle develops between them, so that a faint but undoubted amphiaster is formed (figs. 6, 7). In some preparations the rays on the side toward the nucleus are somewhat heavier than the others and form a distinct cone (fig. 6). This feature is not made out in all cases. A line joining the two blepharoplasts may lie in any position with respect to the nuclear membrane, though the situation shown in fig. 6 is the most usual one. The blepharoplasts continue to separate, moving in paths close to the nuclear membrane, until they lie 180° apart (figs. 8–12). During the earlier stages of the migration the central spindle gradually fades out (fig. 8). The astral radiations persist, and when the blepharoplasts reach polar positions those on the side toward the nucleus become more distinct, being especially conspicuous when the blepharoplasts move a little distance away from the nucleus (fig. 13). They form two cones with the blepharoplasts at their apices, while the radiations extending in other directions remain very faint. The rays of the cone do not diverge from a single point on the blepharoplast, but pass out from a large portion of its surface. At this stage the blepharoplast may reach a diameter of 0.75 μ.

In the nucleus are now seen indications of the approaching mitosis which is to differentiate the spermatids. The nuclear reticulum gradually becomes coarser and eventually resolves itself into a spirem (fig. 14). While the spirem is segmenting to form the chromosomes the nuclear membrane breaks down and the fibers radiating from the blepharoplasts extend into the nuclear cavity and establish the karyokinetic figure. The spindle is extremely

weak in development, so that the relation it bears to the blepharoplasts is not always easily determined at this time. There is no question, however, that the blepharoplasts continue to occupy the poles (fig. 15), as would be expected after the situation in the immediately preceding stages. In the later stages of division many extremely fine strands are present between the daughter nuclei. Whether these are the remains of fibers passing from one blepharoplast to the other or represent the visible effect of the separation of the chromatin upon the cytoplasm was not determined. The cell plate separating the paired spermatids is very late in forming.

During the anaphases of karyokinesis a peculiar change occurs in the blepharoplasts. For a time they lose their affinity for iron-hematoxylin, so that in many preparations treated in the usual way with this stain they may be wholly indiscernable. In more deeply stained cells they appear as translucent bodies considerably larger than during the earlier phases of division (fig. 16). They are no longer solid but contain one or two large vacuoles, which give them in section the appearance of small rings. It is probable that the decrease in staining capacity is due to swelling through the absorption of water without any increase in stainable material. This condition exists only through the remainder of the division; when the sister spermatids are well rounded away from each other the blepharoplasts as a general rule stain deeply again. The vacuole or vacuoles form an irregular cavity, and the whole structure soon takes the form of an uneven ring (figs. 17, 18).

The blepharoplast now breaks up to several pieces which become arranged in a row, usually at once (fig. 19). These pieces multiply rapidly by further fragmentation and form a beaded chain extending about halfway around the nucleus (fig. 21). Fig. 20 shows a mass of these granules just beginning to draw out into a row.

It is at this beaded stage that the cilia begin to develop. From the blepharoplast granules there are seen very fine strands extending toward the periphery of the cell (fig. 21). Whether more than one of the strands, or rudimentary cilia, ever grow out from a single granule was not definitely determined, but since the cilia of the mature spermatozoid and the granules are approximately equivalent in number, it is probable that as a rule each granule gives rise

to one cilium. The further details of cilium development were not worked out.

The blepharoplast granules, which have been lying close together or in contact, now fuse to form a continuous thread. The coalescence usually begins at one end of the chain so that at certain stages it appears solid at one extremity and broken at the other (fig. 22). The union, although intimate, is not so complete that the thread is uniform in diameter throughout, even in the later stages. When the metamorphosis of the spermatid is half complete the beaded nature of the blepharoplast is clearly evident, and when the spermatozoids are mature it still shows an uneven outline.

Immediately after the union of the granules the nucleus begins to show marked changes. It moves to one side of the cell and begins to draw out into a flattened point next to the blepharoplast (fig. 23). At this stage the nucleus and the blepharoplast lie rather close together; the relative position of the two is seen in fig. 24, which represents a portion of a similar cell viewed from the direction *a*. The nucleus continues to elongate and quickly assumes a crescentic form, while its reticulum becomes very coarse and deeply staining (fig. 25). The blepharoplast also lengthens spirally, and the two become widely separated from one another. Figs. 26 and 27 represent respectively an entire cell like that of fig. 25 viewed from the direction *a*, and a section in the plane *ab*. No connections other than the undifferentiated cytoplasm are present between the nucleus and the blepharoplast. The cilia have now increased markedly in length.

As previously noted, the mature spermatozoids vary greatly in size in different antheridia, which may be seen by comparing figs. 28 and 29. The nucleus now stains intensely with iron-hematoxylin. Its surface presents a mottled appearance, while very lightly stained sections show that its interior is quite homogeneous, with several very small vacuoles along the central region. Scattered over the nucleus, mostly along its concave face and occasionally elsewhere in the cytoplasm, are many black globules whose origin and nature were not determined. A few vacuoles are present in the cytoplasm. The blepharoplast continues its spiral growth until it has made about 1.4 turns. The nucleus makes 0.7 of a

turn, but lies parallel to the blepharoplast for 0.44 of a turn, so that the entire spermatozoid makes 1.66 turns. In all of the spermatozoids examined the direction of coiling is the same—from right to left beginning at the innermost end of the blepharoplast when the side of the cell containing the latter is turned toward the observer.

After escape from the antheridium the larger or posterior portion of the nucleus becomes extended and somewhat flattened. Both nucleus and cytoplasm absorb water and show decided enlargement, the cytoplasm, especially in the posterior portion of the spermatozoid, becoming very coarse and foamy through the great enlargement of the vacuoles. Such a mature spermatozoid fixed in the swimming condition over osmic fumes is represented in fig. 30. Exclusive of the cilia it has a length of 19.7 μ.

Discussion

The morphological nature of the blepharoplast is a topic which has been so extensively discussed by STRASBURGER, WEBBER, IKENO, and others that the present writer does not take up the subject with reference to the additional evidence afforded by *Equisetum* without risk, or even necessity, of a certain amount of repetition. In the foregoing historical résumé it was seen that the central point of the discussion has been the question of the possible morphological identity of the centrosome and the blepharoplast. Any analysis of the relationship existing between these two structures must include a consideration of the centrosome as found elsewhere in the plant kingdom, and since it has to do with a cell problem of general interest it should proceed in the light of certain phenomena occurring in the spermatogenesis in animals.

One of the earliest known centrosomes in plants was that discovered by BÜTSCHLI (**10**) in the diatom *Surirella*. It had earlier been seen by SMITH (**77**), who, however, did not recognize its true nature and termed it the "germinal dot." A full account of this centrosome was given by LAUTERBORN (**59**) in his magnificent work on the diatoms, and later by KARSTEN (**57**). It lies near the nucleus, becomes surrounded by radiations, divides and forms the central spindle of the karyokinetic figure in a very peculiar manner.

During karyokinesis it lies near the pole of the broad-poled spindle.

Centrosomes in the Sphacelariaceae have been described by STRASBURGER (**78**), HUMPHREY (**48**), and SWINGLE (**83**). In the vegetative cells of *Sphacelaria* the centrosome, according to STRASBURGER, is situated in a centrosphere at the center of an aster. Previous to mitosis it divides to two which take up positions at opposite poles. In *Stypocaulon* SWINGLE has shown that the centrosome, which lies close to the nucleus, divides, the daughter centrosomes diverging to opposite sides of the nucleus and occupying the spindle poles throughout mitosis. At all stages asters are present. SWINGLE is inclined to regard this centrosome as a permanent organ of the cell.

In the oogonium and segmenting oospore of *Fucus* FARMER and WILLIAMS (**24, 25**) described two centrospheres arising independently 180° apart. In the centrosphere they often observed several granules, but were inclined to attach no importance to them. STRASBURGER (**79**) reported definite centrosomes with asters all through karyokinesis; in the sporeling are stages which indicate that it is a dividing body. He regarded it as a permanent cell organ. In a more recent investigation YAMANOUCHI (**98**) demonstrates in the antheridium and oogonium two very definite centrosomes, which appear independently of each other, become surrounded by conspicuous asters, and occupy the spindle poles during karyokinesis. He further shows that when the sperm reaches the egg nucleus a new centrosome appears on the nuclear membrane at the spot where the sperm entered.

The centrosome of *Dictyota* has been dealt with by two investigators. MOTTIER (**69, 70**) states that in the two divisions in the tetraspore mother cell, in at least the first three or four cell generations of the sporeling and in all the vegetative cells of the tetrasporic plant, a curved rod-shaped centrosome with an aster occurs at the spindle pole. During the early phases of karyokinesis it divides, the daughter centrosomes passing to opposite poles. WILLIAMS (**91**) figures centrosomes and asters essentially like those described by MOTTIER. He also states that the entrance of the sperm causes a centrosome with radiations to appear in the egg cytoplasm.

WOLFE (**94**) found in his study of *Nemalion* that the spindle poles are always occupied, except possibly in the antheridial mitoses, by two heavily staining bodies which he considers centrosomes. They are surrounded by hyaline areas and apparently divide, but no radiations are present.

In *Polysiphonia* (YAMANOUCHI **96**) there are during the prophases of every mitosis two centrosome-like bodies in the kinoplasm at opposite poles of the nucleus. A little later the small bodies disappear, while the kinoplasm takes the form of large centrosphere-like structures without radiations. During the late anaphases these become indistinguishable. YAMANOUCHI believes that these structures are not permanent cell organs, but are formed *de novo* at the beginning of each mitosis.

In the tetraspore mother cell of *Corallina* (DAVIS **19**, YAMANOUCHI **99**) two deeply staining masses, or centrospheres, occur at opposite ends of the nucleus during the prophases of karyokinesis. They occupy the spindle poles and are surrounded by radiations. During the later anaphases they disappear and are formed *de novo* at the next division. No true centrosomes are present.

Among the fungi the best known centrosomes are those of the Ascomycetes. HARPER (**40, 41, 42, 43**) has described in the asci of *Peziza*, *Ascobolus*, *Erysiphe*, *Lachnea*, *Phyllactinia*, and other genera granular disc-shaped centrospheres surrounded by asters at the poles of the spindle. He regards them as permanent organs of the cell. GUILLIERMOND (**37, 38**) shows the presence of centrosomes and asters in several other genera. Especially interesting is the account of *Gallactinia succosa* given by MAIRE (**62**) and later by GUILLIERMOND (**39**). In the ascus of this form a single centrosome arises within the nucleus with a cone of fibers extending toward the chromatin. It divides to two which take up positions 180° apart at the nuclear membrane, at which time asters develop in the cytoplasm. FAULL (**26**) found that in *Hydnobolites* a large centrosome appears outside the nucleus during the prophases of karyokinesis. In *Neotiella* the spindle terminates in minute centrosomes with astral rays very faint or absent. In *Sordaria* he describes the centrosomes as disc-shaped while the cell is in the resting condition and round and smaller during division. The formation of the

spindle was not made out in these three forms. According to SANDS (**73**) the discoid "central body" or centrosome of *Microsphaera* divides with its aster to two which occupy the poles during karyokinesis. In *Humaria rutilans* Miss FRASER (**27**) saw at first two centrosomes lying near each other, each at the apex of a cone of fibers and surrounded by a very faint aster. These move apart and establish the spindle in the usual way. Centrosomes are also figured in *Ascobolus* and *Lachnea* (FRASER and BROOKS **29**). In *Otidea* and *Peziza vesiculosa* (FRASER and WELSFORD **28**) there are distinct centrosomes and asters. The figures given in this paper indicate that division of the centrosome occurs in the latter species. In a recent contribution CLAUSSEN (**16**) figures centrosomes with weakly developed asters in *Pyronema*. The origin of the spindle is not shown.

The first centrosome described in the liverworts was that of *Marchantia* by SCHOTTLÄNDER in 1893 (**75**). According to this observer the centrosome in the spermatogenous cells divides during the anaphases of mitosis, so that each daughter nucleus is accompanied by two. In the gametophytic cells certain minute bodies with radiations at the poles of the elongated nucleus and of the spindle are believed by VAN HOOK (**86**) to represent centrosomes.

Pellia has been the subject of four investigations dealing with the centrosome. In 1894 FARMER and REEVES (**23**) gave an account of mitosis in the germinating spore. They reported two centrospheres at opposite sides of the nucleus with conspicuous radiations but no true centrosomes. The centrospheres occupy the spindle poles and disappear during the telophases of division. DAVIS (**20**) studied the same mitoses and obtained similar results. He states, however, that the centrospheres fade out somewhat earlier. The account given by CHAMBERLAIN (**14**) agrees with these in the essential features. The structures are very distinct in the first mitosis but become less so in the succeeding ones. The most recent work is that of GREGOIRE and BERGHS (**33**). By using improved methods these investigators have found that neither in the resting cells nor during mitosis are there centrospheres or central corpuscles. The centrospheres described by other writers are

shown to be appearances due to the intersection of the very numerous astral radiations at a common point or region. The achromatic figure is derived entirely by the rearrangement of the cytoplasmic network.

As the centrosome becomes more widely known it becomes increasingly difficult to formulate for it any adequate definition. There is scarcely a single attribute common to all true centrosomes; nevertheless there are in general certain features which are fairly characteristic of them as they appear in plants and animals, most prominent among which are the position at the spindle poles with all that this implies, the possession of an aster, and the division to form daughter centrosomes. Because of many exceptions no one of these by itself will definitely determine the morphological nature of a structure possessing it, but when all of them are present we can no longer doubt that we are dealing with a true centrosome.

In a survey of the cilia-bearing structures of bryophytes, pteridophytes, and gymnosperms it is seen that in general the centrosome-like characteristics of the blepharoplast become less and less evident in passing upward through these groups, while the phenomena connected with the bearing of cilia become increasingly prominent. In the bryophytes the conflicting accounts leave us in some doubt concerning the early history of the blepharoplast, but in some cases at least it appears that centrosomes exist through several cell generations and after the last mitosis function as blepharoplasts. In those forms which show them only during the last division they occupy the spindle poles and behave as typical centrosomes. In the spermatids each simply elongates and bears two cilia. In the Filicales, as shown by YAMANOUCHI'S work on *Nephrodium*, the blepharoplast is limited to the last mitosis and does not exhibit the characters of a centrosome, having no division, no radiations, and only occasionally occupying the pole of the spindle. It elongates in intimate union with the spermatid nucleus and bears many cilia. In the gymnosperms the blepharoplast, although surrounded by prominent radiations, appears to play little or no active part in mitosis. In its subsequent behavior it differs widely from the blepharoplasts of the bryophytes and Filicales. After enlarging it becomes vacuolate and breaks up into many fragments, which

arrange themselves in a row and coalesce to form the cilia-bearing band.

The peculiar interest of the phenomena in *Equisetum* is here evident. Although limited to a single mitosis in the antheridium, the blepharoplast retains in its activities the most unmistakable evidences of a centrosome nature, and at the same time shows a metamorphosis strikingly like that in the cycads. In thus combining the main characteristics of true centrosomes with the peculiar features of the most advanced blepharoplasts, it reveals in its ontogeny an outline of the phylogeny of the blepharoplast as it is seen developing through bryophytes, pteridophytes, and gymnosperms, from a functional centrosome to a highly differentiated cilia-bearing organ with very few centrosome resemblances. In *Marsilia* the same pronounced centrosome behavior is shown through at least three cell generations, and in the formation of the cilia-bearing band the cycad situation is foreshadowed, though not to the marked degree seen in *Equisetum*. To the present writer these facts seem to constitute conclusive evidence in favor of the theory advanced by BELAJEFF and by IKENO, that the centrosome has gradually assumed the function of bearing cilia, at the same time losing the usual properties of a centrosome.

The points brought out in such a review are especially suggestive in connection with the conclusions to which WEBBER has been drawn by his studies on *Zamia* (**90**). This investigator emphasizes very strongly the view that the blepharoplast is a distinct organ functioning only as a cilia-former, and urges several objections to its centrosome nature. He points out that it differs from known true centrosomes in not being at the center of an aster at the poles and having no connection with spindle formation, in being limited to a single cell generation, in its great size, in its fragmentation, in its growth into a band, in its function of bearing cilia as far as plant centrosomes are concerned, and in its behavior in fertilization. Although the blepharoplasts of other plant groups are discussed, it appears that these conclusions must have been formulated largely through a consideration of the cycad situation. When the blepharoplast is regarded as an organ developing progressively through bryophytes, pteridophytes, and gymnosperms,

and is treated in the light of analogous phenomena in animals, much of the apparent force of these objections is removed.

In *Marsilia*, as BELAJEFF indicates in his fig. 7 (**7**), and in *Equisetum*, the blepharoplasts are surrounded during the early stages by asters, though these are very weakly developed. When they separate there appears a central spindle, forming with the asters an amphiaster so characteristic of animal cells. In *Equisetum* the radiations persist during the divergence of the blepharoplasts to opposite sides of the cell, and those on the side toward the nucleus remain as the achromatic portion of the karyokinetic figure. The weakness of the other rays or their failure to remain seems to be a matter of secondary importance in the light of spindle-forming activity of this sort. Furthermore, the figures given by zoologists indicate that the occurrence of an aster about the centrosome at the spindle pole is by no means universal in animal cells. In discussing this phase of the question IKENO (**54**) cites the work of MEVES and KORFF (**65**) upon the myriopod *Lithobius forficatus*, in which the spermatocyte centrosomes lie at a considerable distance from the spindle poles during mitosis. The figures given by MEVES and KORFF are strikingly like those of *Ginkgo* (HIRASÉ) and *Cycas* (IKENO).

It is true that the blepharoplast is, as a rule, limited to a single mitosis, but here we must remember the case of *Marsilia* where it is present during three, possibly all four, of the spermatogenous divisions, and also certain liverworts in which a similar condition has been reported. WEBBER accounts for the occurrence of blepharoplasts in all the spermatogenous cell generations in *Marsilia* by considering the latter potential spermatozoids, and thus regards the fact that they appear *de novo* in each cell generation only to disappear at the close of division as a support to his theory of the independent nature of the blepharoplast. If the cells between the central cell of the antheridium and the final spermatids are held to be potential spermatozoids, we should expect, as WEBBER points out, blepharoplasts or their rudiments to be present occasionally. Although these ideas are in accord with the conception of the blepharoplast as an organ *sui generis*, at the same time it does not seem to the present writer that they offer any necessary argument

against its centrosome nature, especially since such "rudiments" as are seen in the spermatogenous cells of *Marsilia* and probably certain liverworts are so remarkably centrosome-like. Moreover, many true centrosomes appear *de novo* in each successive cell generation only to disappear at the close of mitosis.

If the centrosome be an organ which has been practically eliminated from higher plants, we should not be surprised to see it retained, if at all, in different degrees in different plants, and in those cells in which it performs an important biological function, as other workers have suggested. WEBBER's statement that no known plant centrosome has the function of bearing cilia is no longer without a possible exception, since JAHN (**56**) has seen the flagellum of the swarmer of *Stemonitis* growing out from the centrosome during mitosis, exactly paralleling what HENNEGUY (**44**) observed in an insect. That the bearing of cilia is the function which is to be held accountable for the retention of the centrosome in spermatogenous cells seems highly probable. After having lost the usual functions of a centrosome we might well find it appearing still later, in the spermatid itself, as WOODBURN (**95**) believes it does in certain liverworts. BELAJEFF's view concerning the presence of these structures only in the spermatogenous cells is that every cell has its definite "dynamic center," but only in these cases is a staining substance present.

That growth into a band or thread does not deny the centrosome nature of an organ is shown by the great bodily elongation of the inner centrosome in the spermatozoon of *Helix* (KORFF **58**) and certain elasmobranchs (SUZUKI **82,** MOORE **68**). The rodlike centrosome of *Dictyota* and the discoid one of certain ascomycetes constitute a further argument against allowing the character of shape to enter into the definition of the centrosome.

Thus from the standpoint of the theory stated in the foregoing pages, the occurrence of secondary peculiarities developed in connection with cilia-bearing in the cycads and certain pteridophytes, such as large size, fragmentation, and growth into a band, does not distinguish the blepharoplast from the centrosome. This is emphasized by the fact that the first two of these features do not occur in the blepharoplasts of bryophytes and most pteridophytes,

but begin to appear in other members of the latter group, combined with earlier stages in all essential points centrosome-like.

Both WEBBER and STRASBURGER have pointed out that the blepharoplast, since it remains behind in the cytoplasm of the egg and does not meet the female nucleus, is inactive in fertilization, while in animals the centrosome brought into the egg by the spermatozoon plays a very important rôle in fertilization and in the first cleavage mitosis. They advance this as a further evidence that the blepharoplast and the centrosome are not homologous. We have seen that as the blepharoplast has become more and more highly differentiated in relation to the bearing of cilia, it has gradually lost the characters which would serve to mark it as a centrosome. The disappearance of activity during fertilization along with the other usual centrosome functions would be expected, if, indeed, the sperm centrosome of plants ever did take any active part in this process. In *Nephrodium* (YAMANOUCHI **97**) and probably many other pteridophytes and bryophytes the entire spermatozoid enters the egg nucleus, but it is highly improbable that the presence of the blepharoplast in these cases is necessary to fertilization. On the other hand, we cannot yet certainly conclude that a structure is entirely passive in fertilization merely because it does not reach the female nucleus or produce other striking visible effects. In any case it should be remembered that function is not that upon which we can base homology.

In denying the identity of the blepharoplast and the centrosome STRASBURGER (**80**) derives the blepharoplasts of bryophytes, pteridophytes, and gymnosperms from the thickened *Hautschicht* organs of algal swarm spores and gametes. This theory appears to have the support of current conceptions of phylogeny, but it leaves the remarkable behavior of the liverwort, *Marsilia*, and *Equisetum* blepharoplasts to be accounted for. That the *Hautschicht* organ seen in algae should assume, during the course of evolution, such centrosome-like characters, adding them at the earlier end of its life history, seems more difficult of comprehension than the theory stated in the foregoing pages—that the centrosome has gradually taken on the cilia-bearing function.

Through his work on *Marchantia* IKENO was led to state a view which might appear to lessen the contrast between the above two theories. He pointed out (**54**) the resemblance between the elongation of the blepharoplast along the plasma membrane of the *Marchantia* spermatid and the formation of the thickened portion of the *Hautschicht* in the algae as described by STRASBURGER and others, and concluded that this thickening has almost without doubt been derived from a centrosome ontogenetically or phylogenetically, that it is the metamorphosis product of a centrosome. His belief that the basal body in the swarm spore of *Hydrodictyon* is to be accounted for in a similar way was strengthened by the fact that TIMBERLAKE (**85**) observed what were evidently centrosomes at the poles of the spindles giving rise to the spore *Anlage*. In his later paper (**55**) IKENO is less inclined to include the algal *Hautschicht* organs in the same morphological category with the blepharoplasts of the higher plants, but places them in a class apart—"plasmodermal blepharoplasts."

In the light of our limited knowledge of the history of the blepharoplasts in algae it seems wisest to make this disposition of them for the present. Otherwise we should be compelled to assume their homology with those of the higher groups from which they differ so widely in origin, appearance, and general behavior. Since we can no longer remain in doubt concerning the centrosome nature of the blepharoplast of higher plants, this assumption would mean that the alga blepharoplast has lost all centrosome properties and now arises in the motile cell itself in a very modified manner, making it farther advanced in this respect than those of the higher groups, which we can hardly regard as probable. Before any final judgment can be rendered on this question more data must be gathered from the algae themselves, from those forms which show both centrosomes and blepharoplasts in their life histories.

The researches of MOORE (**68**), MEVES (**63, 64**), KORFF (**58**), PAULMIER (**72**), and several others have established beyond question the fact that the centrosome (or centrosomes) of the animal spermatid plays an important rôle in the formation of the motor apparatus of the spermatozoon, the axial filament of the flagellum

growing out directly from it. HENNEGUY (**44**) even observed cilia attached to the centrosomes of the karyokinetic figure in the spermatocyte of an insect.

In comparing the structures of the plant spermatozoid with those of the animal spermatozoon, BELAJEFF (**5**) regarded the blepharoplast, the thread to which it elongates, and the cilia of the former as homologous with the centrosome, middle piece, and tail, respectively, of the latter. The blepharoplast of *Chara* is included in this comparison in spite of the apparent difference in its mode of origin. STRASBURGER (**80**), although agreeing that the body at the base of the flagellum of the animal sperm is a centrosome, homologized only the axial filament of the flagellum with the blepharoplast. This comparison leaves both the cilia of the plant spermatozoid and the centrosome of the animal spermatozoon without counterparts, though a complete homology of this sort is by no means a necessity. The behavior of the centrosomes in the spermatid of *Helix* (KORFF **58**) has made it evident that the axial filament of the flagellum is not a differentiation of the cytoplasm, starting at the centrosome, but is made up of the centrosome substance itself. Thus in comparing the blepharoplast to the axial filament its centrosome relationship is not entirely avoided. In a discussion of this question E. B. WILSON (**92**) regards the work of SHAW and BELAJEFF on *Marsilia* as establishing beyond question the identity of the blepharoplast and the centrosome. He considers the comparison of BELAJEFF as justified and concludes that "the facts give the strongest ground for the conclusion that the formation of the spermatozoids agrees in its essential features with that of the spermatozoa. . . . ."

The deeply staining bodies at the base of the flagella in other ciliated animal cells have also been investigated for further light upon this problem. That they correspond to centrosomes has been rendered highly probable by the work of HENNEGUY (**44**) and LENHOSSEK (**60**), while STUDNICKA (**81**) has obtained evidence apparently in favor of a contrary interpretation. This question must remain with others for further researches to clear up.

In the meantime it should be borne in mind that whatever interpretation is finally put upon the cilia-bearing structures of any

plant or animal group, it must not be forced upon those of all other groups. Since homologies are not determined by function, there is no necessity for expecting all of these organs to belong to the same morphological category. It is in the algae that the blepharoplast of plants at present stands most in need of elucidation. In the bryophytes, pteridophytes, and gymnosperms there can now remain no question that the blepharoplasts are all homologous structures, and that they are, to use IKENO's expression, "ontogenetically or phylogenetically centrosomes."

Summary

1. In the early mitoses in the spermatogenous tissue of *Equisetum* there are no centrosomes, centrospheres, or asters.

2. A minute granule, surrounded by a weakly developed aster, appears in the cytoplasm near the nucleus in each of the cells of the penultimate generation. This granule divides to two, which become the blepharoplasts.

3. The two blepharoplasts, each with its aster, diverge to opposite poles of the nucleus. During the early stages of separation a distinct central spindle develops, so that an amphiaster is present.

4. The astral rays on the side toward the nucleus form two cones of fibers which, when the nuclear membrane breaks down, become the achromatic portion of the karyokinetic figure. The blepharoplasts occupy the poles.

5. During the anaphases and telophases of karyokinesis the blepharoplast enlarges, becomes vacuolate, and breaks up to a number of pieces. After further fragmentation these unite to form the cilia-bearing thread.

6. In the metamorphosis of the spermatid the nucleus and blepharoplast elongate spirally side by side, but have no connection other than that afforded by the undifferentiated cytoplasm.

7. The activities of the blepharoplast in *Equisetum*, taken together with the behavior of recognized true centrosomes in plants and analogous phenomena in animals, are believed to constitute conclusive evidence in favor of the theory that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes.

The investigation here recorded was carried on under the direction of Professor JOHN M. COULTER, Dr. CHARLES J. CHAMBERLAIN, and Dr. W. J. G. LAND, to whom the writer wishes to express his sincere thanks. He is also greatly indebted to Dr. SHIGÉO YAMANOUCHI for many helpful suggestions.

THE UNIVERSITY OF CHICAGO

LITERATURE CITED

1. BELAJEFF, W., Ueber Bau und Entwickelung der Spermatozoiden der Gefässkryptogamen. Ber. Deutsch. Bot. Gesells. **7**:122–125. 1888.
2. ———, Ueber Bau und Entwickelung der Spermatozoiden der Pflanzen. Flora **79**:Ergänzab.:1–48. *pl. 1.* 1894.
3. ———, Ueber den Nebenkern in spermatogenen Zellen und die Spermatogenese bei den Farnkräutern. Ber. Deutsch. Bot. Gesells. **15**:337–339. 1897.
4. ———, Ueber die Spermatogenese bei den Schachtelhalmen. *Idem* **15**:339–342. 1897.
5. ———, Ueber die Aehnlichkeit einiger Erscheinungen in der Spermatogenese bei Thieren und Pflanzen. *Idem* **15**:342–345. 1897.
6. ———, Ueber die Cilienbildner in den spermatogenen Zellen. *Idem* **16**:140–144. *pl. 7.* 1898.
7. ———, Ueber die Centrosome in den spermatogenen Zellen. *Idem* **17**:199–205. *pl. 15.* 1899.
8. BOLLETER, E., *Fegatella* (L.) *corda.* Eine morphologisch-physiologische Monographie. Beih. Bot. Centralbl. **18**:327–408. *pls. 12, 13.* 1905.
9. BUCHTIEN, O., Entwicklungsgeschichte des Prothalliums von *Equisetum.* Bibliotheca Botanica **8**:1–49. *pls. 1–6.* 1887.
10. BÜTSCHLI, O., Ueber die sogenannten Centralkörper der Zelle und ihre Bedeutung. Verhandl. des Naturhist.-Med. Vereins zu Heidelberg. N.F. **4**:535–538. 1891.
11. CALDWELL, O. W., *Microcycas calocoma.* Bot. Gaz. **44**:118–141. *pls. 10–13.* 1907.
12. CAMPBELL, D. H., Zur Entwickelungsgeschichte der Spermatozoiden. Ber. Deutsch. Bot. Gesells. **5**:120–127. *pl. 6.* 1887.
13. CHAMBERLAIN, C. J., The homology of the blepharoplast. Bot. Gaz. **26**:431–435. 1898.
14. ———, Mitosis in *Pellia.* Decennial Publ. Univ. of Chicago **10**:329–345. *pls. 25–27.* 1903.
15. ———, Spermatogenesis in *Dioon edule.* BOT. GAZ. **47**:215–236. *pls. 15–18.* 1909.
16. CLAUSSEN, P., Zur Entwicklungsgeschichte der Ascomyceten. *Pyronema confluens.* Zeitschr. Bot. **4**:1–64. *pls. 1–6. figs. 13.* 1912.

17. DANGEARD, P. A., Mémoire sur les Chlamydononadinées ou l'histoire d'une cellule. Le Botaniste **6**:65–290. *figs. 19.* 1898.
18. ———, Étude sur la structure de la cellule et ses fonctions. Le *Polytoma uvella*. *Idem* **8**:5–58. *figs. 4.* 1901.
19. DAVIS, B. M., Kerntheilung in der Tetrasporenmutterzelle bei *Corallina officinalis* L. var. *mediterranea*. Ber. Deutsch. Bot. Gesells. **16**:266–272. *pls. 16, 17.* 1898.
20. ———, Nuclear studies in *Pellia*. Ann. Botany **15**:147–180. *pls. 10, 11.* 1901.
21. ———, Spore formation in *Derbesia*. *Idem* **22**:1–20. *pls. 1–2.* 1908.
22. ESCOYEZ, E., Blepharoplaste et centrosome dans le *Marchantia polymorpha*. La Cellule **24**:247–256. *pl. 1.* 1907.
23. FARMER, J. B., and REEVES, J., On the occurrence of centrospheres in *Pellia epiphylla*, Nees. Ann. Botany **8**:219–224. *pl. 14.* 1894.
24. FARMER, J. B., and WILLIAMS, J. L., On fertilization, and the segmentation of the spore in *Fucus*. *Idem* **10**:479–487. 1896.
25. ———, Contributions to our knowledge of the Fucaceae; their life history and cytology. Phil. Trans. Roy. Soc. London B **190**:623–645. *pls. 19–24.* 1898.
26. FAULL, J. H., Development of ascus and spore formation in ascomycetes. Proc. Boston Soc. Nat. Hist. **32**:77–113. *pls. 7–11.* 1905.
27. FRASER, H. C. I., Contributions to the cytology of *Humaria rutilans*. Ann. Botany **22**:35–55. *pls. 4, 5.* 1908.
28. FRASER, H. C. I., and WELSFORD, E. J., Further contributions to the cytology of the ascomycetes. *Idem* **22**:465–477. *pls. 26, 27.* 1908.
29. FRASER, H. C. I., and BROOKS, W. E. St. J. Further studies on the cytology, of the ascus. Ann. Botany **23**:538–549. 1909.
30. FUJII K. (Has the spermatozoid of *Ginkgo* a tail or not?). Bot. Mag. Tokyo **12**:287–290. 1898. (Japanese.)
31. ——— (On the morphology of the spermatozoid of *Ginkgo biloba*). *Idem* **13**:260–266. *pl. 7.* 1899. (Japanese.)
32. ——— (Account of a sperm with two spiral bands). *Idem* **14**:16–17. 1900. (Japanese.)
33. GREGOIRE, V., and BERGHS, J., La figure achromatique dans le *Pellia epiphylla*. La Cellule **21**:193–238. *pls. 1, 2.* 1904.
34. GRIGGS, R. F., The development and cytology of *Rhodochytrium*. BOT. GAZ. **53**:127–173. *pls. 11–16.* 1912.
35. GUIGNARD, L., Developpement et constitution des anthérozoides. Rev. Gén. Bot. **1**:11–27, 63–78, 136–145, 175–194. *pls. 2–6.* 1889.
36. ———, Centrosomes in plants. BOT. GAZ. **25**:158–164. 1898.
37. GUILLIERMOND, M. A., Recherches sur la karyokinèse chez les ascomycètes. Rev. Gén. Bot. **16**:129–143. *pls. 14, 15.* 1904.
38. ———, Remarques sur la karyokinèse des ascomycètes. Ann. Mycol. **3**:344–361. *pls. 10–12.* 1905.

39. GUILLIERMOND, M. A., Aperçu sur l'évolution nucléaire des ascomycetes et nouvelles observations sur les mitoses des asques. Rev. Gén. Bot. **23**:89–121. *figs. 1–8. pls. 4, 5.* 1911.

40. HARPER, R. A., Beitrag zur Kenntniss der Kerntheilung und sporenbildung im Ascus. Ber. Deutsch. Bot. Gesells. **13**:(67)–(68). *pl. 27.* 1895.

41. ———, Kerntheilung und freie Zellbildung im Ascus. Jahrb. Wiss. Bot. **30**:249–284. *pls. 11, 12.* 1897.

42. ———, Cell division in sporangia and asci. Ann. Botany **13**:467–525. *pls. 24–26.* 1899.

43. ———, Sexual reproduction and the organization of the nucleus in certain mildews. Publ. Carnegie Inst. No. 37. Washington, 1905.

44. HENNEGUY, L. F., Sur les rapports des cils vibratiles avec les centrosomes. Arch. Anat. Mikr. **1**:481–496. *figs. 5.* 1898.

45. HIRASÉ, S., Notes on the attraction spheres in the pollen cells of *Ginkgo biloba*. Bot. Mag. Tokyo **8**:359. 1894.

46. ——— (On the spermatozoid of *Ginkgo biloba*). *Idem* **10**:325–328. 1896. (Japanese.)

47. ———, Untersuchungen über das Verhalten des Pollens von *Ginkgo biloba*. Bot. Centralbl. **69**:33–35. 1897.

48. HUMPHREY, J. E., Nucleolen und Centrosomen. Ber. Deutsch. Bot. Gesells. **12**:108–117. *pl. 6.* 1894.

49. HUMPHREY, H. B., The development of *Fossombronia longiseta* Austr. Ann. Botany **20**:83–108. *pls. 5, 6. figs. 8.* 1906.

50. IKENO, S., Vorläufige Mittheilung über die Spermatozoiden bei *Cycas revoluta*. Bot. Centralbl. **69**:1–3. 1897.

51. ———, Zur Kenntniss des sogenannten centrosomähnlichen Körpers im Pollenschlauche der Cycadeen. Flora **85**:15–18. 1898.

52. ———, Untersuchungen über die Entwickelung der Geschlechtsorgane und den Vorgang der Befruchtung bei *Cycas revoluta*. Jahrb. Wiss. Bot. **32**:557–602, *pls. 8–10.* 1898.

53. ———, Die Spermatogenese von *Marchantia polymorpha*. Beih. Bot. Centralbl. **15**:65–88. *pl. 3.* 1903.

54. ———, Blepharoplasten im Pflanzenreich. Biol. Centralbl. **24**:211–221. *figs. 1–3.* 1904.

55. ———, Zur Frage nach der Homologie der Blepharoplasten. Flora **96**: 538–542. 1906.

56. JAHN, E., Myxomycetenstudien. 3. Kernteilung und Geisselbildung bei den Schwärmern von *Stemonitis flaccida* Lister. Ber. Deutsch. Bot. Gesells. **22**:84–92. *pl. 6.* 1904.

57. KARSTEN, G., Die Auxosporenbildung der Gattungen *Cocconeïs*, *Surirella*, und *Cymatopleura*. Flora **87**:253–283. *pls. 8–10.* 1900.

58. KORFF, K. VON, Zur Histogenese der Spermien von *Helix pomatia*. Arch. Mikr. Anat. **54**:291–296. *pl. 16.* 1899.

59. LAUTERBORN, R., Untersuchungen über Bau, Kernteilung, und Bewegung der Diatomeen. Leipzig. 1896.

60. LENHOSSEK, M. VON, Ueber Flimmerzellen. Verh. Anat. Gesell. in Kiel. **12**:106. 1898.

61. LEWIS, C. E., Embryology and development of *Riccia lutescens* and *Riccia crystallina*. BOT. GAZ. **41**:109–138. *pls. 5–9.* 1906.

62. MAIRE, R., Recherches cytologiques sur quelques ascomycètes. Ann. Mycol. **3**:123–154. *pls. 3–5.* 1905.

63. MEVES, F., Ueber Struktur und Histogenese der Samenfäden von *Salamandra maculosa*. Arch. Mikr. Anat. **50**:110–141. *pls. 7, 8.* 1897.

64. ———, Ueber Struktur und Histogenese der Samenfäden des Meerschweinchens. *Idem.* **54**:329–402. *pls. 19–21. figs. 16.* 1899.

65. MEVES, F., and KORFF, K. VON, Zur Kenntniss der Zelltheilung bei Myriopoden. Arch. Mikr. Anat. **57**:481–486. *pl. 21. figs. 5.* 1901.

66. MIYAKE, K., On the centrosome of Hepaticae. Bot. Mag. Tokyo **19**:98–101. 1905.

67. ———, The spermatozoid of *Ginkgo*. Jour. Appl. Micr. and Lab. Methods **5**:1773–1780. *figs. 10.* 1906.

68. MOORE, J. E. S., Structural changes in the reproductive cells during spermatogenesis of elasmobranchs. Quart. Jour. Micr. Sci. **38**:275–313. *pls. 13–16.* 1895.

69. MOTTIER, D. M., Das Centrosom bei *Dictyota*. Ber. Deutsch. Bot. Gesells. **16**:123–128. *figs. 5.* 1898.

70. ———, Nuclear and cell division in *Dictyota dichotoma*. Ann. Botany **14**:166–192. *pl. 11.* 1900.

71. ———, The development of the spermatozoid in *Chara*. Ann. Botany **18**:245–254. *pl. 17.* 1904.

72. PAULMIER, F. C., The spermatogenesis of *Anasa tristis*. Jour. Morph. **15**:Suppl. 223–272. *pls. 13, 14.* 1899.

73. SANDS, M. C., Nuclear structure and spore formation in *Microsphaera*. Trans. Wis. Acad. Sci. **15**:733–752. *pl. 46.* 1907.

74. SCHAFFNER, J. H., The centrosomes of *Marchantia polymorpha*. Ohio Naturalist **9**:363–388. 1908.

75. SCHOTTLÄNDER, P., Beiträge zur Kenntniss des Zellkerns und der Sexualzellen bei Kryptogamen. Beitr. Biol. Pflanzen Cohn **6**:267–304. *pls. 4, 5.* 1893.

76. SHAW, W. R., Ueber die Blepharoplasten bei *Onoclea* und *Marsilia*. Ber. Deutsch. Bot. Gesells. **16**:177–184. *pl. 11.* 1898.

77. SMITH, H. L., A contribution to the life history of the Diatomaceae. Proc. Am. Soc. Micr. Pts. I and II. 1886–1887.

78. STRASBURGER, E., Schwärmsporen, Gameten, pflanzliche Spermatozoiden, und das Wesen der Befruchtung. Hist. Beitr. **4**:49–158. *pl. 3.* 1892.

79. ———, Kerntheilung und Befruchtung bei *Fucus*. Jahrb. Wiss. Bot. **30**:351–374. *pls. 27, 28.* 1897.

80. ———, Ueber Reduktionsteilung, Spindelbildung, Centrosomen, und Cilienbildner im Pflanzenreich. Hist. Beitr. **6**:1–224. *pls. 1–4.* 1900.

81. STUDNICKA, F. K., Ueber Flimmer- und Cuticularzellen mit besonderer Berücksichtigung der Centrosomenfrage. Sitzungsber. Königl. Bömisch. Gesell. Wiss. Math.-Naturwiss. Classe. No. 35. 1899.

82. SUZUKI, B., Notiz über die Entstehung des Mittelstückes von Selachiern. Anat. Anz. **15**:125–131. *figs. 6.* 1898.
83. SWINGLE, W. T., Zur Kenntniss der Kern- und Zelltheilung bei den Sphacelariaceen. Jahrb. Wiss. Bot. **30**:296–350. *pls. 15, 16.* 1897.
84. THOM, C., The process of fertilization in *Aspidium* and *Adiantum*. Trans. Acad. Sci. St. Louis **9**:285–314. *pls. 36–38.* 1899.
85. TIMBERLAKE, H. G., Development and structure of the swarm spores of *Hydrodictyon*. Trans. Wis. Acad. Sci. **13**:486–522. *pls. 29, 30.* 1902.
86. VAN HOOK, J. M., Notes on the division of the cell and nucleus in liverworts. BOT. GAZ. **30**:394–399. *pls. 2, 3.* 1900.
87. WEBBER, H. J., Peculiar structures occurring in the pollen tube of Zamia. BOT. GAZ. **23**:453–459. *pl. 40.* 1897.
88. ———, The development of the antherozoid of *Zamia*. *Idem* **24**:16–22. *figs. 5.* 1897.
89. ———, Notes on the fecundation of *Zamia* and the pollen tube apparatus. of *Ginkgo*. *Idem* **24**:225–235. *pl. 10.* 1897.
90. ———, Spermatogenesis and fecundation in *Zamia*. U.S. Dept. Agri., Bureau Plant Ind., Bull. No. **2**:1–100. *pls. 1–7.* 1901.
91. WILLIAMS, J. L., Studies in the Dictyotadeae. II. The cytology of the gametophyte generation. Ann. Botany **18**:183–204. *pls. 12–14.* 1904.
92. WILSON, E. B., The cell in development and inheritance. p. 175. 1900.
93. WILSON, M., Spermatogenesis in the Bryophyta. Ann. Botany **25**:415–457. *pls. 37, 38. figs. 3.* 1911.
94. WOLFE, J. J., Cytological studies on *Nemalion*. *Idem* **18**:607–630. *pls. 40, 41. fig. 1.* 1904.
95. WOODBURN, W. L., Spermatogenesis in certain Hepaticae. *Idem* **25**:299–313. *pl. 25.* 1911.
96. YAMANOUCHI, S., The life history of *Polysiphonia violacea*. BOT. GAZ. **42**:401–449. *pls. 19–28.* 1906.
97. ———, Spermatogenesis, oogenesis, and fertilization in *Nephrodium*. *Idem* **45**:145–175. *pls. 6–8.* 1908.
98. ———, Mitosis in *Fucus*. *Idem* **47**:173–197. *pls. 8–11.* 1909.
99. ———, The life history of *Corallina*. Unpublished.

EXPLANATION OF PLATES VII AND VIII

All figures were drawn at the level of the table with the aid of an Abbé camera lucida under a Zeiss apochromatic objective 2 mm. N.A. 1.40, with compensating ocular 18. They have been reduced one-third in reproduction, and now show a magnification of 2533 diameters.

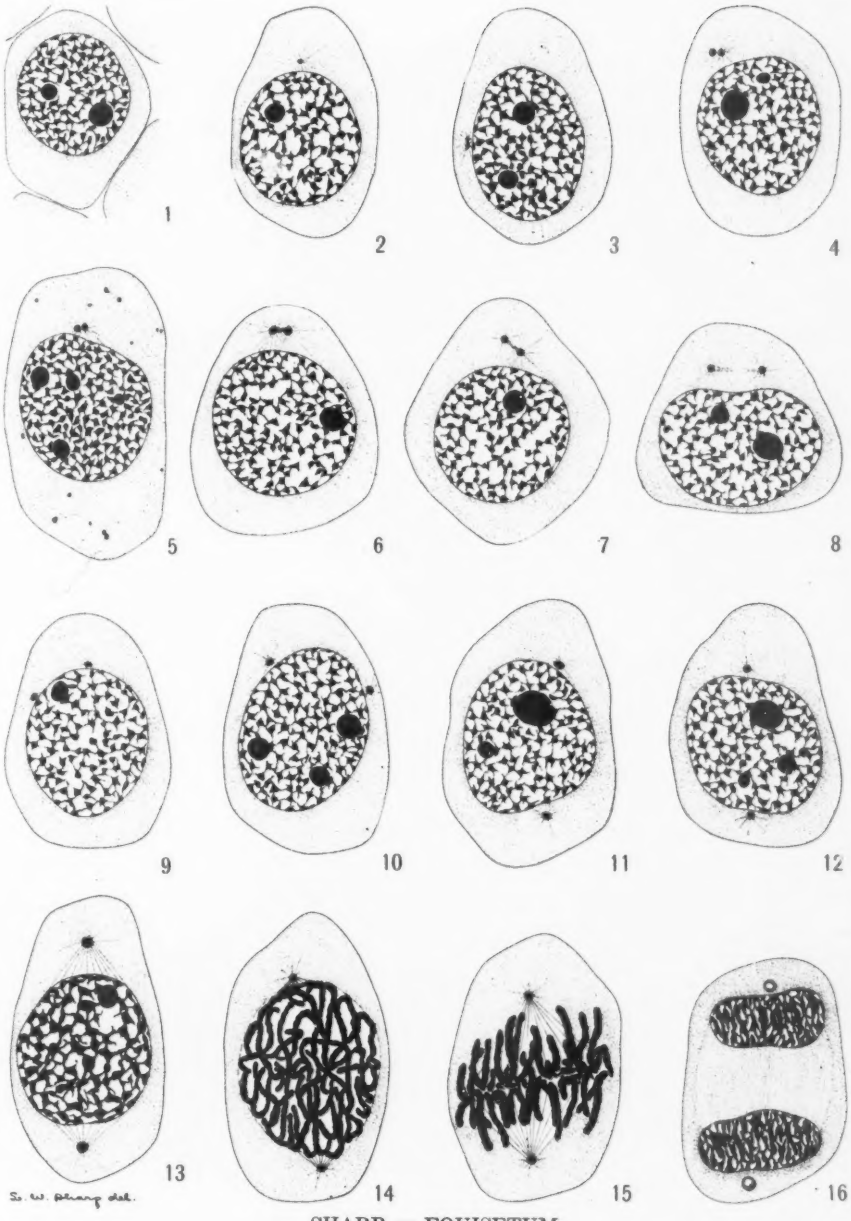
PLATE VII

FIG. 1.—Cell of penultimate generation rounding off.

FIG. 2.—Deeply staining body with faint aster present in cytoplasm.

FIG. 3.—Division of small body in cytoplasm.

FIG. 4.—Two blepharoplasts formed by division of the original body.



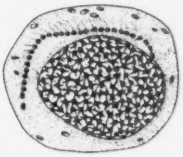
SHARP on EQUISETUM

17

18

19

20



21

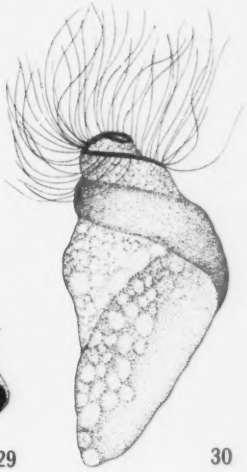
22

26

23

24

25



30

27

E. W. Sharp del.

28

29

SHARP on EQUISETUM

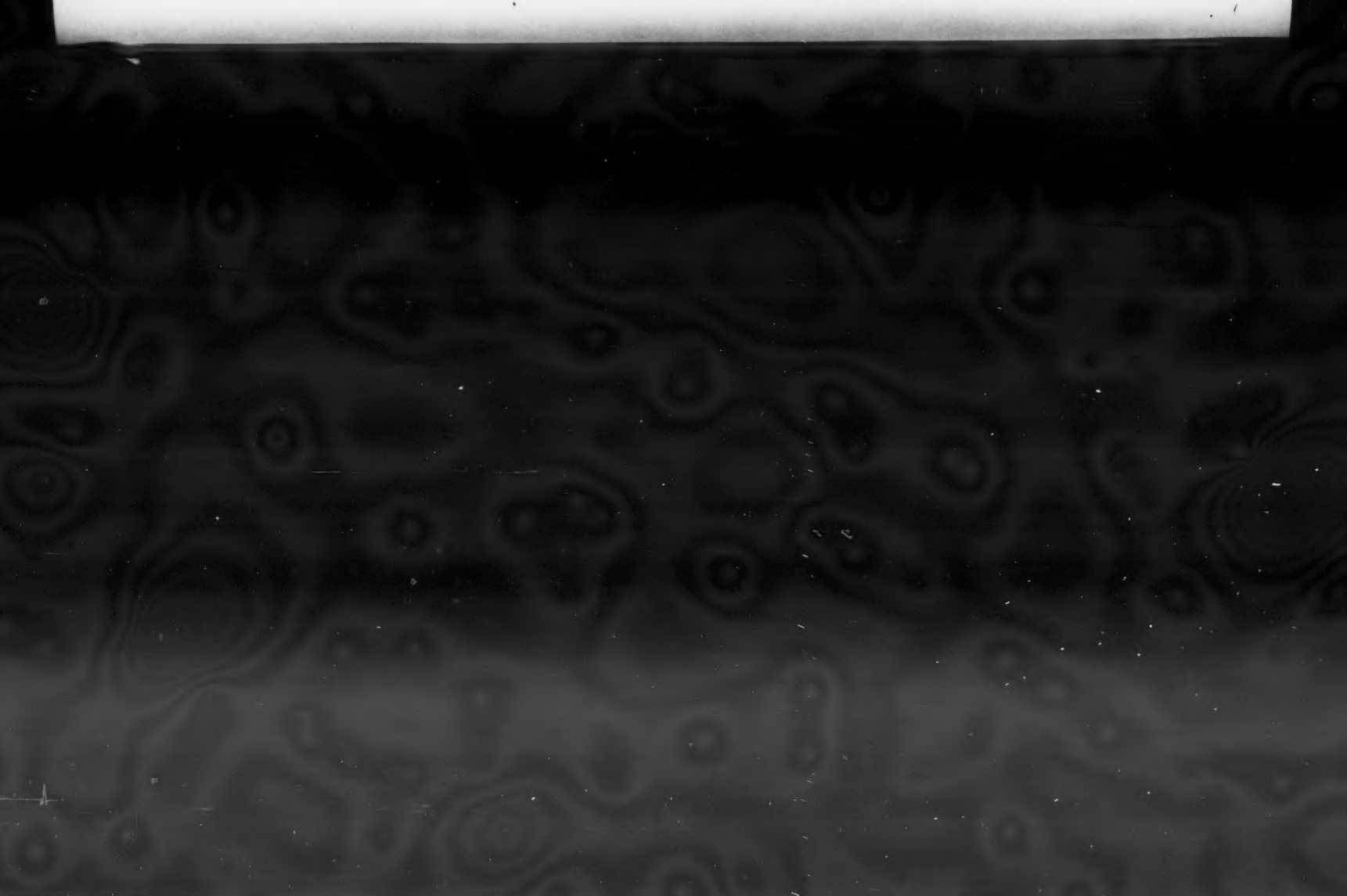


FIG. 5.—Blepharoplasts at upper side of nucleus; other single and paired bodies present in cytoplasm; exceptional condition.

FIG. 6.—Blepharoplasts beginning to separate; central spindle present; the radiations on the side toward the nucleus form a distinct cone.

FIG. 7.—Later stage; no cone of rays present.

FIG. 8.—Still later stage; central spindle fading out.

FIGS. 9–12.—Stages in the divergence of the blepharoplasts.

FIG. 13.—Blepharoplasts lying at a greater distance from nucleus; the radiations on the side toward the nucleus form two well marked cones; the chromatin network becoming coarser.

FIG. 14.—Spirem stage: nuclear membrane beginning to break down; astral rays much shorter.

FIG. 15.—Late prophase: the spindle fibers have been formed from the radiations of the blepharoplasts, which occupy the poles.

FIG. 16.—Telophase: blepharoplasts have enlarged and become vacuolate.

PLATE VIII

FIG. 17.—Pair of spermatids differentiated: blepharoplasts have the form of irregular rings; plastids present in cytoplasm.

FIG. 18.—Spermatid: blepharoplast beginning to fragment.

FIG. 19.—Blepharoplast broken up to several pieces.

FIG. 20.—Granules formed by fragmentation of blepharoplast beginning to draw out into a row; nucleus again in resting condition.

FIG. 21.—Blepharoplast granules arranged in a long row; cilia beginning to grow out from them; plastids present.

FIG. 22.—Blepharoplast granules fusing at right end of chain; still separate at left end; degenerating plastids in cytoplasm.

FIG. 23.—Blepharoplast now a continuous thread; cilia partially developed; nucleus beginning its metamorphosis.

FIG. 24.—Portion of a similar cell viewed from the direction *a*, showing proximity of nucleus and blepharoplast; cilia not drawn.

FIG. 25.—Later stage: nucleus and blepharoplast have elongated spirally; chromatin network very coarse.

FIG. 26.—Entire cell similar to that of fig. 25 viewed from the direction *a*, showing independence of nucleus and blepharoplast; cilia not drawn.

FIG. 27.—Section of similar cell in plane *ab*: *n*, nucleus; *b*, blepharoplast; cilia not drawn.

FIG. 28.—Mature spermatozoid still in antheridium: the blepharoplast makes 1.4 turns, the nucleus 0.7 of a turn; deeply staining globules in cytoplasm near nucleus.

FIG. 29.—Smaller spermatozoid in another antheridium, viewed from a different direction.

FIG. 30.—Spermatozoid fixed in the swimming state over osmic fumes: the dark spiral band bearing the cilia is the blepharoplast; the lighter, homogeneous portion the nucleus; the vacuolate portion the cytoplasm; length exclusive of cilia, 19.7 μ.

THE PRIMARY COLOR-FACTORS OF LYCHNIS AND COLOR-INHIBITORS OF PAPAVER RHOEAS[1]

GEORGE HARRISON SHULL

The frequency with which the presence of hereditary characters is dominant over their absence naturally suggests that inhibiting factors may be operating when the reverse relation appears to exist, as when the hornless character of polled cattle dominates over horns, and the "smooth" character over the "bearded" in wheat, oats, etc. Some writers (DAVENPORT, BATESON, PUNNETT) have even taken the extreme view that dominance is in all cases a criterion of "presence." That this position is untenable I have shown several years ago (SHULL **11, 12**), and CASTLE (**2**) also opposes such an idea, calling attention to WOOD's well known sheep hybrids (WOOD **15**), in which the horned condition is dominant in the male and hornlessness in the female offspring from the same cross, as a proof that no such sweeping generalization is permissible. It may be granted, however, that presence is *usually* dominant, and that the dominance of the apparent absence of a character is probably in most cases, but not in all, the dominance of an inhibiting factor over its own absence. It is only necessary to keep the mental reservation that in any single instance of a putative inhibitor another hypothesis is always available, namely, that the gene for the character that is supposed to be inhibited, when existing singly as in the heterozygote, may be nearly or quite incapable of reaching the threshold of visible expression.

Both of the characters mentioned above by way of example—the polled condition in cattle and the lack of long awns in wheat—are structural characters. When a *color*-character is inhibited, the

[1] Under the title "Inhibiting factors in *Lychnis* and *Papaver*," this paper was read before the Botanical Society of America, Washington, D.C., December 28, 1911. The change of title and slight changes in the text have been rendered necessary by the discovery that the purple-flowered male parent of family 10201 discussed below was probably heterozygous in both the primary factors for color. This discovery in no wise affects the general considerations presented in the paper as read, but it withdraws *Lychnis dioica* for the present as an example of dominant white.

result is a "dominant white" if the inhibition of all pigmentation is practically complete, or there may result parti-colored forms exhibiting various color-patterns, or the dominance of what appears to be a lower grade of pigmentation over a higher grade when the inhibition is localized or otherwise incomplete.

One of the earliest known and most familiar examples of dominant white is found in the plumage of domestic fowl, in most breeds of which white is epistatic to all colors, but not always quite perfectly so. It was soon found, however, that not all of the plumages of white fowl are of the same nature, for the "Silkie" fowl's white plumage is recessive to colors. Dominant and recessive whites have been discovered in a number of other cases, both in plants and in animals. BATESON (**1**, p. 105) and GREGORY (**7**) found that white-flowered primulas with red stems are dominant whites, while those with green stems are recessive whites;[2] KEEBLE, PELLEW, and JONES (**9**), and Miss SAUNDERS (**10**) have demonstrated dominant and recessive whites in *Digitalis purpurea;* and EAST (**4**, pp. 81 f.) has shown that an inhibitor for blue aleurone-color exists in some maize plants though absent in others.

In many cases, perhaps generally, the inhibition is not quite complete, and dominant whites are often distinguishable by the possession of patches or washings of color not found in recessive whites. Similar incompleteness of action of inhibitors is seen in the occasional appearance of rudimentary horns or "scurs" in pure-bred polled cattle, in the development of a few feathers on the legs of pure clean-legged fowls, the production of short awns or "beards" on "smooth" wheat, oats, etc.

Not only are there dominant and recessive whites, but there are also different kinds of these, dependent upon the fact, now well known, that the same visible effect may be attained in various ways. It has been demonstrated that pigmentation is generally due to the interaction of at least two independent factors. When only two such factors are required, e.g., *C* and *R*, there may be three kinds of recessive whites, one lacking *C*, one lacking *R*, and

[2] While this is the general rule, KEEBLE and PELLEW (**8**) have found exceptions in the variety "Pearl," which has dominant white flowers and green stems, and in "Snow King," in which both dominant and recessive whites were found associated with dark red stems.

one lacking both *C* and *R;* and each of these whites will behave differently in certain crosses, though all are recessive to colors and may be quite indistinguishable from one another when pure-bred. Individuals lacking either *C* or *R*, when crossed with other individuals having the same genotypic constitution, or when crossed with individuals of the third type, which lack both *C* and *R*, will produce only white offspring; but when recessive whites of the first two types are crossed together, the complementary factors, *C* and *R*, necessary for the production of color, are brought together and a colored F_1 results, as exemplified by the classic case of "Emily Henderson" sweet peas, in which two white-flowered plants, differing externally only in the form of the pollen-grains, produced "reversionary" purple offspring when crossed together. Many similar "reversions" have been discovered by experimental breeders in a considerable number both of plants and of animals, and the old riddle of "reversion on crossing," exemplified by these phenomena, has been given a satisfactory solution in the "factor hypothesis." In so many organisms have different kinds of recessive whites been found, that their discovery in additional species no longer occasions surprise.

Less is known of the chemistry of dominant whites, but it is conceivable that these may also be of several kinds. It is plain that any pigment which is readily converted into an allied colorless compound would give a basis for a dominant white in which the pigment nucleus coexists with a factor which changes it to its colorless derivative. A suggestive illustration *in vitro* of such a reaction is the ready reduction of indigo blue ($C_{16}H_{10}N_2O_2$) in alkaline solutions to indigo white ($C_{16}H_{12}N_2O_2$). SPIEGLER (**14**) believed that he had succeeded in isolating a "white melanin" from white wool and white horsehair, and while GORTNER (**5, 6**) has been unable to confirm SPIEGLER'S conclusions in this regard, the general type of reaction suggested by SPIEGLER may be retained as possibly explaining some cases of dominant white. GORTNER (**5**) has proposed a very different hypothesis, namely, that as melanin is the product of an oxidase acting on a chromogen (tyrosin), dominant whites may be the result of anti-enzymes which inhibit the action of the oxidase. The same hypothesis is applicable to

the widely distributed plant-pigment anthocyanin, whose method of origin appears to be in essential agreement with that of melanin. More recently GORTNER (**6**) has shown that anti-enzymes are not necessary for the inhibition in question, as the oxidizing action of tyrosinase is prevented by the presence of small quantities of such relatively simple *m*-dihydroxyl phenolic compounds as orcin, resorcin, and phloroglucin. GORTNER shows that on the basis of his investigations a satisfactory explanation can be given of those rare cases in which a white is dominant in some crosses and recessive in others, as apparently exemplified by the Shirley poppies described below.

I have been making numerous crosses among strains of *Lychnis dioica* L., and during the past six years have grown about 660 pedigreed families of this species. Nearly 300 of these families have resulted from matings between white-flowered individuals, many of the matings having been arranged for the specific purpose of finding different kinds of whites possessing complementary color-factors. Until the past summer (1911) all of these crosses between white-flowered parents have given uniformly white-flowered progenies,[3] and a similar number of crosses between white and colored individuals have invariably shown the whites to be recessive to colors, though they differed genotypically in that some of the whites carried a factor for reddish-purple and others a factor for bluish-purple, the red being epistatic to blue.

With the bringing in of two new strains of *Lychnis dioica* from their native habitats in Germany (for seeds of which I am indebted to Dr. BAUR), I have realized the complementary factors for color for which I had been looking thus far in vain.[4]

[3] The several purple-flowered individuals from white-flowered parents, mentioned in an earlier paper (SHULL **13**), appear now to have been plus-fluctuants of a "tinged white" which had not been recognized as such at the time that paper was written. They have no bearing on the problem of complementary color-factors here under consideration.

[4] That the several kinds of recessive whites exist among my Cold Spring Harbor strains, though I have not yet made a mating among them between two whites which resulted in a purple-flowered F_1, is sufficiently demonstrated by the facts presented in my earlier paper. My failure thus far to secure a purple-flowered F_1 from two whites among these strains must be due to the mere chance that I have not selected whites from the proper families.

These two forms of *Lychnis* from Germany are with apparent good reason classified by German taxonomists as distinct species, the white-flowered form being called *Melandrium album* Garcke, and the purple-flowered form *M. rubrum* Garcke. *Melandrium album*, as it appears in my cultures, has relatively narrow, spatulate, moderately ascending rosette-leaves of a rather dull dark green; the corollas are white, slender, and long-exserted from the calyx-tube; the styles are long and slender, with inconspicuous stigmatic papillae. The plants are easily grown as annuals by early sowing. *Melandrium rubrum* Garcke, grown under the same conditions, has the rosette-leaves broader, with more rounded apices; the leaves are nearly horizontal, a little darker green, and more shining. The corollas are reddish-purple, shorter, scarcely extending beyond the mouth of the calyx; the styles shorter and relatively heavy, with prominent stigmatic papillae. A very small percentage of the plants are forced to bloom as annuals, even when seeds are sown early in February. In so far as visible characters are concerned, these two forms have shown but slight fluctuations, except that in *M. album* the calyx varies from plain green through green striped with purple to a rather deep dull crimson. They have kept quite distinct from each other in regard to the characteristics enumerated, but because they breed together with undiminished fertility and because I have many other strains showing similar differences and various degrees of intermediacy, I must continue for the sake of convenience the use of the Linnean name (*Lychnis dioica*) for the entire aggregation. To what extent the other forms in my cultures may have been derived from hybridizations between *M. album* and *M. rubrum* cannot be surmised, but all strains which I have thus far found in America have presented one or more characteristics which are not directly traceable to either of the German forms, nor obviously derivable from them by recombinations of their characters. For instance, my original material of this species, collected at Cold Spring Harbor, has considerably lighter green foliage than either *M. album* or *M. rubrum*, and from the vicinity of Harrisburg, Pa., I have secured a "chlorina" (CORRENS **3**) variety having light yellow-green foliage.

Three crosses were made in 1910 between the German *Melan-*

drium album and my original white-flowered strain from Cold Spring Harbor. Two of these families (10200 and 10202) were the result of crossing two different German white-flowered females with pollen from a single Cold Spring Harbor white-flowered male. Both of these matings produced only white-flowered offspring, totaling 182 individuals. The young seedlings were indistinguishable from Cold Spring Harbor seedlings of the same age, but later they became darker green and were intermediate between the parents. A third family (1068) was essentially reciprocal to the two just described, being produced by crossing a female sib of the male used in 10200 and 10202 with pollen from a German white-flowered male. The 77 offspring were vegetatively indistinguishable from the reciprocal families, but the flowers were all reddish-purple. These different results in supposedly reciprocal crosses probably indicate that there was an unsuspected heterogeneity in the German strain. That the difference was due to heterogeneity in the Cold Spring Harbor parental family is rendered improbable by the fact that a mating (1060) between the female used as the mother of 1068 and the male used as the father of 10200 and 10202 resulted in a progeny of 73 white-flowered plants. It is unfortunate that a similar check was not applied to the German plants entering into these families, by also crossing them together. The only cross (10203) made between two specimens of *M. album* resulted in 84 offspring, all white-flowered. The mother of this family was also the mother of 10202, but the father was not the same as the father of 1068.

Several crosses were also made between the purple-flowered German *Melandrium rubrum* and my Cold Spring Harbor strains, both white-flowered and purple-flowered. Families 1092 and 1093 were produced by crossing a single white-flowered female of the Cold Spring Harbor strain with two males of *M. rubrum*, one derived from seeds collected at Furtwangen in the Schwarzwald, and the other from Oefingen in Baden. A female sib of the last-mentioned plant (i.e., from Baden) was crossed (10204) with pollen from a white-flowered sib of the mother of families 1092 and 1093. It represented a cross, therefore, as nearly reciprocal to 1093 as is possible in dioecious material. Two other families

(10206 and 10207) were produced by crossing two females grown from the Baden seeds with pollen of a single pure-bred purple-flowered male from Cold Spring Harbor. As *Melandrium rubrum* has reddish-purple flowers and as this color has been shown to be epistatic to bluish-purple (which may have been carried as a latent character by the white-flowered plants), there was no reason to expect that the F_1 progeny of any of these five crosses would present any noticeable difference in flower-color from that of their *M. rubrum* parent. This expectation was realized, the 262 offspring from these crosses all having reddish-purple flowers. The young plants in these families were generally indistinguishable from pure-bred *M. rubrum*, but later they differed by being notably more vigorous, having enormous rosettes of broad, shining, dark-green leaves. They were also much more easily grown as annuals by early sowing, being in this regard intermediate between the parents. Almost all of the hybrids were blooming by the middle of July, before the first flowers of any pure *M. rubrum* had opened.

Compared with these crosses between *Melandrium rubrum* and the Cold Spring Harbor plants, a cross of *M. rubrum* with *M. album* gave a totally different and unexpected result. A mating between a female of the white-flowered *album* and a purple-flowered male *rubrum* produced an F_1 (10201) consisting of 23 white-flowered individuals and 3 (probably 4) purple-flowered ones. The white-flowered plants were unlike either parent in vegetative characters, having relatively short, sharp-pointed, grayish-green leaves which were strongly ascending in the fully developed rosette, while both parents have long, spreading, dark-green leaves. The flowers were not only white like those of their white-flowered mother, but they were also nearly identical with them in form. It was noted that rarely some of the flowers became faintly and unevenly streaked and washed with purple just as they were fading, a feature never observed in the flowers of any of my other white-flowered plants. These white-flowered hybrids were a little later in blooming than their white-flowered parent, but were still easily induced by early sowing to behave as annuals. The purple-flowered offspring of this cross were of an altogether different character, and were not readily distinguishable in rosette and

floral characters from their purple-flowered male parent. They were also like pure *M. rubrum* in not blooming until late in the season. One plant having a rosette identical with those of the three purple-flowered specimens remained a rosette, but will doubtless have purple flowers if it survives the winter.[5]

Why there should be this segregation of types in the F_1, and why one of these types should so completely resemble the male parent, while the other type was goneoclinic to the female parent, though abundantly distinct from it in the rosettes, are mysteries. Perhaps this unexpected segregation of characters in a putative F_1 is further evidence of the heterogeneity of the *M. album* material. If the white-flowered mother were heterozygous in a dominant white factor, the expected result of a cross with *M. rubrum* would be 3 white-flowered to 1 purple-flowered, or in this particular family 20 white-flowered to 7 purple-flowered, to which expectation the observed result is in sufficiently close agreement considering the small number of individuals. The same result would be attained if the *rubrum* parent were heterozygous in respect to both the primary factors for color, *C* and *R*, it being assumed that the *album* parent lacked both these factors. No other evidence of heterogeneity in *M. rubrum* has yet appeared in my cultures. It should be remarked that neither of these German strains had been pedigreed in controlled cultures, but were simply collected in separate regions in nature, so that questions as to their genotypic purity are legitimate.

In the derivatives of the corn-poppy (*Papaver Rhoeas* L.), among which are the dainty and beautiful "Shirley" poppies of our gardens, color-inhibitors are also found. According to his own statement, Rev. W. WILKS was first induced to pursue the course of selection, which resulted in the strain known as the "Shirley poppies," by discovering a bud-variation on a wild corn-poppy growing in a corner of his garden. Several flowers on this plant differed from the rest in having petals with a narrow white margin. Such a white margin is now a frequent feature of garden poppies, and when appropriate crosses are made, it is found that the presence

[5] Note added June 5, 1912. This plant is now blooming and has purple flowers as predicted.

of a margin is dominant over its absence. It is probable, therefore, that the white margin is due to the presence of an inhibitor whose action is localized in the margins of the petals.

In 1911, among 73 pedigreed families of *Papaver Rhoeas* grown at the Station for Experimental Evolution, 45 resulted from crosses between plants of which the presence or absence of a margin had been recorded, and of which a goodly proportion of the offspring were capable of being similarly recorded. The rest either had one white-flowered parent whose possession (or lack) of a margin could not be determined by inspection, or for some other reason one or both parents or the offspring could not be safely characterized with respect to margins. Of the 45 families having the margins of parents and offspring recorded, 3 represented crosses between plants both of which had margined petals, 17 were from crosses between one margined and one unmargined parent, and 25 resulted from matings between plants none of which had margined petals. The three families from matings between margined parents consisted of 236 individuals, including in each family a mixture of plants with margined and with unmargined petals. Records of the margins were often impossible, owing to the interference of other factors not yet fully investigated, so that the numbers of each type of offspring have no special significance in the present connection and they will be reserved for discussion at another time.

Of the 17 families produced by mating plants with margined and with unmargined petals, 12 were composed of a mixture of plants, some with margins and some without, 3 contained only plants with unmargined petals, and in 2 families practically all of the individuals had margins. With margins dominant over their absence, only two kinds of families were to be expected from this type of mating, namely, all margined if the margined parent chanced to be homozygous, and mixtures of plants with margined and unmargined petals if the margined parent was heterozygous. The three families (10272, 10273, 10274) in which no margins appeared, though one of the parents had a margin, are exceptions. One margined individual was the mother of all three of these exceptional families. The records show that this plant differed

from the usual type, the margin being in this case red-violet[6] instead of nearly white. Whether this red-violet margin was a purely somatic modification of the dark-red body-color, or whether it was germinal, it was clearly of a different nature from the white margins involved in the other families.

In the two families (10287, 10289) whose margined parents were evidently homozygous, a small number of plants were recorded without margins. These exceptional plants occurred among those set into the garden, while larger numbers of plants from the same families, which were grown to maturity in pots in the propagating-house, were all margined. In family 10287 there were 6 plants with unmargined petals among 40 grown to maturity in the garden, and none among 133 which flowered in pots, and in family 10289 one was noted as unmargined among 47 plants in the garden and none among 83 which developed in pots. However these seven unmargined specimens are to be accounted for, it is clear that each of these families is the offspring of a homozygous margined parent.

In the 25 matings between plants, neither of which possessed margined petals, there appeared only 15 plants with margins among a total of 1402 offspring, and in a number of those recorded as margined the margin was merely a trace of lighter color of more or less doubtful character. Only in one family (10291) were the margins unmistakable, and in this family the margined plants occurred only among those which were retained in the greenhouse. Of 21 which matured in the garden none had margins, while among 99 which flowered in pots in the greenhouse there were 10 with margins, several having only a trace, while others had well marked white margins 2 mm. wide—in one plant 3 mm. wide. No attempt need be made at present to account for these few margined plants, for their number is too small to vitiate the conclusion that the unmargined condition is recessive, and that typically all the offspring of two unmargined parents are unmargined.

The most interesting matings in which margins were involved

[6] The color-nomenclature adopted in this paper is based on the spectrum colors, as arranged in the Milton Bradley system. Exact shades and tints have been recorded, but for the sake of simplicity these have not been reproduced here.

were those in which the wild poppy was crossed with its garden derivatives, for as already noted the margin is a new character which does not normally occur in the wild poppy. In the two families representing such matings, the wild poppy was used as the mother in 10298 and as the father in 10310. Both families consisted of mixtures of margined and unmargined plants, showing conclusively here also that margined petals is a dominant character, since the wild plants are certainly homozygous in the lack of such margins. The dominance of the margined condition of the garden poppies over the unmargined condition of their wild prototype is in marked contrast to all the other color-characters of *Papaver Rhoeas* yet investigated, for the dark red-orange body-color[7] of the wild poppy is epistatic to all the body-colors presented by the numerous garden forms. If dominance were a secure criterion of the presence of a gene which is absent in the recessive type, these results would indicate that while the various body-colors of the garden forms originated as retrogressive mutations, i.e., by losses of characters, the white margins of the petals represent a progressive mutation through the addition of a gene which inhibits the development of color in that region. Doubleness also proves to be dominant over the single type of the wild poppy, and, on the basis of the same assumption, would have to be classed as a progressive mutation. I cannot forbear, however, to repeat the caution that dominance does not necessarily demonstrate the progressiveness of a mutation, since the alternative hypothesis, mentioned above in the first paragraph, allows for the dominance of a character which has originated by a retrogressive mutation.

There is still one other color-inhibitor (possibly several) in the derivatives of *Papaver Rhoeas*, which is in some respects more noteworthy than that which produces the white margins. This affects the body-color of the petals, producing what is essentially a dominant white, though in this case the inhibition is not usually complete and the flowers often show some irregular striation of dull violet, reddish, or bluish color on the petals, especially in the presence of purple stamens.

[7] By the expression "body-color" it is intended to indicate the color of the general intermediate region of the petals as distinct from "center" (proximal) and "margin" (distal).

A single white-flowered plant with yellow stamens was crossed in 1909 with three red-flowered plants (yielding families 10275, 10281, 10282) and with two plants having dull striations on the petals (families 10280, 10283), and the offspring of these five matings were generally white or whitish-flowered. Of 559 plants in these families only 25 were neither pure white nor white with traces of reddish color, and of these 25, all that had a full red (i.e., not striated) parent were lighter in color than that parent. These fully pigmented offspring may simply represent minus-fluctuations in the action of the inhibitor derived from the white-flowered parent. If this is the correct interpretation of these few plants with colored flowers, it should be possible to secure from them progenies displaying the presence of the inhibitor though it be invisible in both parents. While I have as yet grown no offspring from the colored plants of these families, I have two other families (10270, 10308) in which the same whitish offspring have appeared, though both parents in each case were fully pigmented. Family 10270 was produced by mating two dark-red parents which were sibs in a family consisting of red, red-orange, pink (light violet-red), and white. The progeny of these two dark-red plants consisted of 68 white or whitish and 70 pigmented, the latter often striated and generally much less intensely pigmented than either parent. Only two of the offspring showed as deep shade as that of their parents. The parents of family 10308 were also red-flowered sibs in a family containing red, red-orange, pink, and white. They were considerably lighter red than the parents of 10270, but were fully and evenly pigmented. Their offspring consisted of 80 white- and whitish-flowered plants and 13 with pigmented flowers, none of which were as deeply pigmented as either parent, and several of which showed the peculiar striation which seems to be one of the manifestations of the inhibitor believed to be operating in these crosses. Similar results were obtained in seven families (10266, 10273, 10274, 10297, 10303, 10305, 10311) produced from mating together two plants with striated petals, or a striated with a plain red, and only in one family, containing three individuals (10268), did the "dominant white" fail to manifest itself in progenies from matings of this character. In the latter family a

cross between a light-red and a striated individual produced three offspring, all with flowers slightly darker red than those of their red-flowered parent. Considering the complexity of some of these families, this number of individuals is entirely inadequate for the deduction that family 10268 was really exceptional.

While I have laid no emphasis thus far on the fact, it may have been noted that all of these poppy-families in which a "dominant white" has made its appearance have been derived from red or striated parents, never from red-orange or pink (light violet-red). It seems that the factor under discussion is not a general inhibitor of color but only of pure spectrum-red. The following facts seem to prove this: The same white-flowered plant with yellow stamens which we have seen producing white-flowered progenies when mated with red (families 10275 and 10281) was also mated with two homozygous pink-flowered plants (families 10277 and 10278) and a homozygous red-orange plant (10279) and in all of these three crosses the white-flowered parent proved to be a recessive white. Families 10277 and 10278 consisted of 43 pink-flowered and 25 red-flowered plants, and 10279 contained 226 red-orange-flowered plants and 1 red-flowered. Not a single individual in any of these three families had white or whitish flowers. In keeping with these results are families in which striated plants were mated with pink (10295) and red-orange (10301), for in neither of these families appeared a white-flowered offspring or one with striations, 10295 yielding 37 pink-flowered and 33 red-flowered and 10301 giving 22 which were red-orange and 5 intermediate between this and red.

The occurrence of many red-flowered plants in these families, when one of the parents supposedly contained an inhibitor for red, is not satisfactorily explainable on the assumption made above, that there is a single inhibitor for red whose effectiveness fluctuates to such an extent that its presence may not be detected in its extreme minus-fluctuations. An alternative hypothesis may be suggested, which must await further experimentation for its confirmation or rejection. If there be two factors, *A* and *B*, which are ineffective when existing apart from each other, but which become an inhibitor when acting together, the observed

results could be explained by assuming that in those matings which produced whitish-flowered offspring, the one parent possessed *A*, the other *B*, while in those matings in which a fully pigmented progeny was produced, the two parents had the same factor—either both *A* or both *B*—or else one of them lacked both *A* and *B* and the other parent lacked one of them. The occurrence of fully pigmented individuals in association with "dominant whites" need not then be minus-fluctuations of a single inhibitor, but might be the result of segregation of inhibiting factors, one or more of which were heterozygous in one or both parents.

Summary

Dominant and recessive whites have been discovered in a number of different plants and animals. Both the dominant whites and the recessive whites may be of different kinds, though externally indistinguishable.

Dominance does not necessarily indicate presence of an added gene, but when the absence of a character appears to be dominant over its presence, the action of an inhibiting factor may usually be inferred. An alternative hypothesis is always available, however, which should prevent a too dogmatic assertion that dominance is synonymous with presence.

A white-flowered form (*Melandrium album*) of *Lychnis dioica* L. from Germany, when crossed with the purple-flowered form (*M. rubrum*) from the same country, produced 23 white-flowered and 4 purple-flowered offspring, but in certain crosses with a white-flowered strain derived from plants growing at Cold Spring Harbor, the German white-flowered plants produced purple-flowered offspring in the F_1, in other crosses only white-flowered offspring were produced.

In the "Shirley" poppies (*Papaver Rhoeas* L.), the presence of a white margin of the petals is a dominant character and is probably due to an inhibitor limited in its effective action to the margins of the petals.

These white margins and doubleness of the flowers are the only characters in the garden poppies which were found dominant over the corresponding characters of the wild type from which they

were derived. They may represent the results of progressive mutations, but here again caution is necessary because of the alternative hypothesis.

There is also an inhibitor which affects the body of the petals in the "Shirley" poppies, producing what is essentially a dominant white, though the inhibition is often very imperfect, in which case the flowers are more or less washed and striated with color, though generally whitish.

This supposed inhibitor was evident only in crosses involving at least one red-flowered or striated parent. The same white-flowered plant which was a dominant white in crosses with red-flowered and striated plants was a recessive white in crosses with pink-flowered and red-orange-flowered plants.

In several cases red-flowered plants crossed together produced a whitish progeny and a similar result was produced when two striated plants were mated or when striated was crossed with red.

Two hypotheses to account for these facts are considered: (*a*) that there is one inhibitor affecting only the pure spectrum-red and having no effect on pink and red-orange; the minus-fluctuations of this inhibitor pass the limit of visibility; (*b*) that there are two factors, *A* and *B*, which have no visible effect when existing alone, but which act as an inhibitor when brought together. These two hypotheses must be tested by further breeding.

I take pleasure in acknowledging here the faithful work of Mr. E. E. BARKER, who assisted me in making the records upon which this paper is based.

STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, L.I.

LITERATURE CITED

1. BATESON, W., Mendel's principles of heredity. Cambridge: University Press. 1909.
2. CASTLE, W. E., Heredity in relation to evolution and animal breeding. New York: D. Appleton & Co. 1911.
3. CORRENS, C., Vererbungsversuche mit blass(gelb)grünen und buntblättrigen Sippen bei *Mirabilis Jalapa*, *Urtica pilulifera*, und *Lunaria annua*. Zeitschr. Ind. Abst. Vererb. **1**:291–329. *figs. 2*. 1909.

4. EAST, E. M., Inheritance in maize. Bull. 167, Conn. Agr. Exp. Sta. pp. 142. *pls. 25.* 1911.
5. GORTNER, R. A., Spiegler's "white melanin" as related to dominant and recessive whites. Amer. Nat. **44**:497. 1910.
6. ———, Studies on melanin: III. The inhibitory action of certain phenolic substances upon tyrosinase. Jour. Biol. Chem. **10**:113–122. 1911.
7. GREGORY, R. P., Experiments with *Primula sinensis.* Jour. Genetics **1**:73–132. *pls. 3. figs. 2.* 1911.
8. KEEBLE, F., and PELLEW, Miss C., White-flowered varieties of *Primula sinensis.* Jour. Genetics **1**:1–5. 1911.
9. KEEBLE, F., PELLEW, Miss C., and JONES, W. N., The inheritance of peloria and flower-color in foxgloves (*Digitalis purpurea*). New Phytol. **9**:68–77. *fig. 1.* 1910.
10. SAUNDERS, Miss E. R., On inheritance of a mutation in the common foxglove (*Digitalis purpurea*). New Phytol. **10**:47–63. *pl. 1. figs. 14.* 1911.
11. SHULL, G. H., The "presence and absence" hypothesis. Amer. Nat. **43**:410–419. 1909.
12. ———, A simple chemical device to illustrate Mendelian inheritance. Plant World **12**:145–153. *pl. 1. fig. 1.* 1909.
13. ———, Color inheritance in *Lychnis dioica* L. Amer. Nat. **44**:83–91. 1910.
14. SPIEGLER, E., Ueber das Haarpigment. Beitr. Chem. Physiol. Path. **4**:40. 1904.
15. WOOD, T. B., Note on the inheritance of horns and face-color in sheep. Jour. Agr. Sci. **1**:364. 1906.

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. XI

NEW PLANTS FROM IDAHO

AVEN NELSON

(WITH TWO FIGURES)

The papers in this series numbered IX and X both dealt with novelties secured by Mr. J. FRANCIS MACBRIDE, of New Plymouth, Idaho, in his collections of 1910. The region that proved of greatest interest during that season was certain portions of Owyhee County in the southwestern part of the state. However, he found it possible to visit other counties, and in all of them much of interest was secured.

He spent the season of 1911 also in the field, revisiting some of the favored localities at earlier dates, and going into new fields later in the season. The writer found it possible to join MACBRIDE in his work during the month of July, at which time certain of the lava lands of southern Idaho were investigated. A few days were spent also in the Sawtooth and in the Lemhi National forests. This and a succeeding paper will deal with some of the many interesting things that were found. The plants to be sent out will bear MACBRIDE'S numbers, but those secured while both were in the field will have both collectors' names upon the labels.

Sisyrinchium inalatum, n. sp.—Roots coarsely fibrous, inordinately numerous from the small cormlike rhizome, widely spreading: stems simple, tufted and crowded, erect, 3–4 dm. high, rather stout, wholly wingless, leafy below, more than twice as long as the longest leaf, about 10-striate: leaves 9–15-nerved, hyaline-margined at the middle only where they are often 6–8 mm. broad, the upper half somewhat divergent, either straight or somewhat arcuate: the outer spathe large and conspicuous, 4–6 cm. long, many-nerved, at its widest part (where it is more or less scarious-margined) 8–10 mm. broad, tapering gradually to the apex, usually surpassing even the mature umbel by nearly half (sometimes more),

the upper one-fourth closed: inner spathe 6–8-nerved, with intermediate nerves, the whole margin broadly hyaline, less than half as long as the outer and shorter than the mature pedicels: scales thin, silvery scarious, from half to nearly as long as the inner spathe, the primary one with 3 conspicuous green nerves: flowers 1–4, medium size, seemingly purple or purplish (the material at hand quite mature and the flowers out of condition): stamineal column short: pedicels erect, 25–45 mm. long: capsules 5–6 mm. long, obovoid-globose but evidently trigonous, pale green: seeds about 15, 2 mm. long, flattened-oval, sometimes slightly trigonous or rhomboidal but always compressed and more or less wing-margined, and rugulose-pitted.

It is not clear to what species this is most nearly allied, but it is so strongly marked by its mass of fibrous roots, its stout wingless stems, its broad leaves and spathes, and its large capsule and numerous large winged seeds, that its recognition is not difficult.

MACBRIDE'S no. 909, Silver City, June 17, 1911, is the only collection at hand. This, singularly enough, was secured on a dry open hillside.

Eriogonum shoshonensis, n. sp.—Annual, 1–2 dm. high, more or less white-lanate throughout and densely so on the under side of the leaves: stems few to several from the base, slender, dichotomously or tricotomously branched, the lower internode rather long, the succeeding ones gradually shorter, all the branches rather closely erect and therefore appearing fasciculately crowded above: leaves open-rosulate, 1–2 cm. long, on slender petioles as long or longer: bracts minute, triangular-subulate: involucres sessile, in the forks and lateral, and rather numerous on the branchlets, firm and somewhat angled by the thickened greenish nerves that terminate in the very short teeth, nearly tubular, about 2 mm. long, 5–10-flowered: perianth glabrous, on slender unjointed filiform pedicels which protrude about 1 mm.; perianth segments pinkish-white, with greenish midrib, obovate, obtuse, 2 mm. long, the outer noticeably broader than the inner: achene ovoid-triangular, abruptly contracted into a rather slender beak, nearly as long as the body, both together as long as the perianth.

Probably most nearly allied to *E. truncatum* T. & G. Proc. Amer. Acad. **8**:173, but differing essentially in habit. That may perhaps best be described

as stemless, with a short stout peduncle from the summit of which spring few–several foliar-bracted rays which are then dichotomous or trichotomous. The involucre of that species is tubular campanulate.

Secured by NELSON and MACBRIDE at Shoshone, Idaho, in the rich lava soil of sagebrush swales, July 18, no. 1186.

Polygonum emaciatum, n. sp.—Very slender glabrous silver-green annual, 15–40 cm. high: stem usually simple below but branching dichotomously from near the base and upward, the internodes rather long, noticeably geniculate at the nodes so as to give the stems and branches a zigzag aspect: leaves few, linear, revolute, short, or even reduced to mere bracts: sheaths scarious, irregularly lacerate into a few acuminate awns: flowers in slender, rather open, terminal, spicate racemes; 1 or 2 in the axils of the small bracts which are more or less concealed by the lacerate sheaths; pedicels short, slender, erect, not exserted: perianth segments obovate-cuneate, whitish with a red line, about 3 mm. long: ovary oblong, triangular, as long as the slender styles: mature fruit not at hand.

This suggests *P. tenue* Michx., from which its peculiar skeletonized appearance, its zigzag branching, its very small not cuspidate leaves, and its usually solitary white flowers easily separate it.

The type is MACBRIDE'S no. 1692, "doby" lava slopes, near Sweet, Idaho, August 14, 1911; also by JUNE CLARK, August 18, no. 269, in the same locality.

Loeflingia verna, n. sp.—A diminutive, vernal, glabrous annual, 1–5 cm. high, with short filiform root: stem simple or with few-several filiform ascending branches: leaves triangular-subulate, not cuspidate, 2 mm. or less long, opposite at the few nodes: flowers few, solitary-axillary on rather long filiform pedicels forming an open few-flowered cyme: sepals 5, entire, about 3 mm. long, lanceolate, acute, scarious-margined, 1-nerved but neither carinate nor setaceous tipped: petals usually wanting, if present scarious, narrowly lanceolate, as long as the sepals, apparently 3 only: stamens 3 or rarely 5: anthers small, on capillary filaments, stigmas 3 (or 2?), subsessile but distinct: ovary several-ovuled; capsule 1-celled, ovoid-triangular, as long as the sepals: seeds attached to the central-basal placenta on rather long funiculi: embryo moderately curved, accumbent.

It is interesting to add another American species to this singularly erratic genus. I have no doubt that the describer of *L. pusilla* Curran was right in her observation "stamens 5," in spite of the fact that later observers have noted only 3. The plants now at hand show this tendency to vary the number of stamens, and occasionally to develop petals also. Is the following statement of the manuals correct, "ovules attached laterally," or does the wording in this description come closer to the fact?

Secured by MACBRIDE in the grass among the sagebrush, on the plains near New Plymouth, April 24, 1911, no. 773.

ARABIS LIGNIPES **impar,** n. var.—Larger and coarser than the species (*A. lignipes* A. Nels. BOT. GAZ. **30**:191. 1900), the lignescent caudex apparently more enduring, often 8–10 cm. high and marked only by the scalelike leaf bases: pubescence extending to the inflorescence and mature pods.

The type of this variety is MACBRIDE'S no. 828, dry, stony slopes, on Squaw Creek, Sweet, Idaho, May 8, 1911. I refer here also specimens by C. N. WOODS, Hailey, Idaho, no. 9*a*, 1910.

DRABA LAPILUTEA A. Nels. in Coult. & Nels. Man. 222. 1909. *D. yellowstonensis* A. Nels. BOT. GAZ. **30**:189. 1900.—Fine specimens of this strongly marked species were secured by NELSON and MACBRIDE on a high mountain near Mackay. It accords very closely with the type except that some of the specimens indicate that it may sometimes at least be perennial. The flowers are truly white and not merely so on fading.

Draba McCallae and *D. columbiana* Rydb., Bull. Torr. Bot. Club **29**:241. 1901, are very near allies, if indeed they be not both referable to *D. lapilutea*.

Parrya Huddelliana, n. sp.—Perennial from very long slender flexible woody roots which penetrate far down among the rocks in subalpine slides: caudex of few–several very slender (almost filiform) somewhat scaly branches which elongate (even to several dm.) sufficiently to bring the herbage out among the surface rocks: leaves rosulate on the tips of the branches of the caudex, with some scales or petioles for a few cm. below, narrowly spatulate-oblanceolate, 12–25 mm. long, somewhat cinereous with a stellately branched pubescence: inflorescence a short crowded corymbose raceme almost hidden among the leaves but the pedicels elongating in fruit, the few–several large pods appearing umbellate upon rays 10–15 mm. long: pods oblong or bicuneate, 2–3 cm. long, the acute

apex tipped with the short, slender, obscurely lobed stigma, very flat, with perfect septum and the few large seeds in two rows: seeds oval, silvery-white, with a crisped or cellular seed-coat.

To find so perfect an example of a true *Parrya* in this region was a most agreeable surprise. It is nearer to *P. arctica* R. Br. than to *P. macrocarpa* R. Br.

This fine species was discovered by COLUMBUS I. HUDDLE, supervisor of the Lemhi National Forest, Mackay, Idaho. It was growing in the loose black-limestone slide-rock, in Bear Canyon, altitude about 10,000 feet. The specimens, secured in good quantity, were in full fruit. The species is named for its discoverer, to whose courtesy the writer owes the memory of a glorious summer day's splendid collecting in the forest, under Mr. HUDDLE's watchful supervision, July 30, 1911. Distributed under NELSON and MACBRIDE's no. 1466.

CHYLISMA SCAPOIDEA **seorsa,** n. var.—Annual or winter annual, green and glabrous in appearance but minutely puberulent on stems and in the inflorescence: stems branching from the base and upward, 2–3 dm. high, equally leafy up to the rather long naked open raceme, the basal leaves falling away sooner than the upper: leaves oblong to ovate or even obovate, entire or denticulate with callous-tipped teeth.

The best example of this at hand is AVEN NELSON's no. 4125, Evanston, Wyo., July 27, 1897. NELSON and MACBRIDE's no. 1145, King Hill, July 16, 1911, is also referable to this variety.

Taraxia tikurana, n. sp.—Perennial from long, and in older plants, rather thick fleshy roots with 1–3 crowns, strictly acaulescent, green but under a lens sparsely and minutely appressed hirsutulous: leaves 8–15 cm. long (including the petiole), narrowly oblanceolate in outline, pinnately deeply and irregularly toothed, the rounded sinuses often extending to the midrib; the slender petiole shorter than the blade: flowers rather numerous, yellow; the calyx tube 6–10 cm. long, slender: calyx lobes narrowly lance-oblong, about 8 mm. long, twice as long as the obconic tube: petals large, obovate, emarginate or rounded, 10–14 mm. long: stamens unequal, the shorter stamens only about half as long as the others; anthers attached about one-third of their length from the base: capsule small, subulate, ridged by the rounded sutures; seeds in two rows, irregularly oblong.

This splendid species is nearest to *T. breviflora* Nutt., from which it is so different that there is no need to emphasize the differences.

MACBRIDE secured it in Jordan Valley, near Silver City, June 22, 1911; NELSON and MACBRIDE'S no. 1302, from Tikura, Blaine Co., is taken as the type. It seems to occur in the rich soil of river bottoms.

Cicuta cinicola, n. sp.—From a thick stout root (?)[1] widely and freely branched, 2 m. (more or less) high: leaves large; the lower often 1 m. long, bipinnate with some of the larger pinnae trifoliate, gradually reduced and simplified upward, the uppermost very small and trifoliate or simple; the leaflets of the lower leaves from ovate to broadly lanceolate, 12–20 cm. long including the long stout petioles, coarsely serrate, the teeth broadly triangular and abruptly apiculate; upward the leaflets become gradually smaller and narrower, the uppermost lance-linear and only 2–3 cm. long; involucre wanting or of a few green or rarely scarious-margined bracts, or sometimes a single foliar bract 2–4 cm. long: pedicels numerous, 3–7 mm. long; the involucels of many lance-linear, scarious-margined bractlets, as long as or longer than the pedicels: fruit strongly compressed laterally, the dorsal diameter twice as great as the lateral, about 3 mm. long, the stylopodium low-conical, the styles about 1 mm. long: the carpels somewhat oblique at base and more or less inequilateral: the low rounded ribs in surface display about equally the intervals in which lie the large irregular solitary oil tubes; commissural face plane, rather narrow, with two smaller oil tubes (fig. 1).

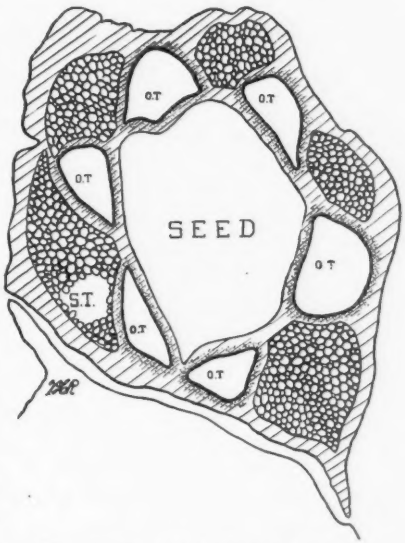


FIG. 1.—*Cicuta cinicola* A. Nels., n. sp.

[1] The root was not collected, but the impression of the collectors is that it was too large and deep-set to be removed with the means at hand.

This species is singularly like *C. Bolanderi* Wats., except for the much larger leaves and the large broad leaflets. The fruit, however, is much more flattened dorsally and the pericarp much thickened with strengthening tissue. It is extremely improbable, however, that the species heretofore supposed to be restricted to the tide-land marshes of Suisun, Cal., should next appear in the lava lands of Idaho.

The plants are large, stately, well branched, and conspicuous objects among the underbrush that borders Rock Creek, near Twin Falls. The stem at the base is often 4–5 cm. in diameter. The soil in this neighborhood is the well known volcanic ash that has proven so well suited to the production of apples. NELSON and MACBRIDE'S no. 1315, July 25, 1911, is the type.

Cynomarathrum Macbridei, n. sp.—Glabrous: acaulescent: root woody, surmounted by a branched caudex which is clothed

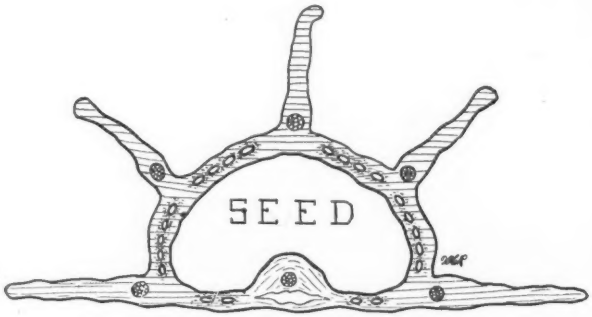


FIG. 2.—*Cynomarathrum Macbridei* A. Nels., n. sp.

with dead leaf bases: leaves narrowly oblong, bipinnate, 3–7 cm. long including the very slender petiole; the pinnae often pinnately cleft; the leaflets elliptic, very numerous and minute, only 1–2 mm. long: scapes 1–3 times as long as the leaves, slender: the flowers closely capitate in a small cluster, white: rays few and short (only a few mm.) even in fruit: pedicels nearly wanting: seeds flattened dorsally, all of the ribs thin-winged, the lateral more than half as broad as the body, the others not much narrower: oil tubes 3–5 in the intervals, 4–8 on the commissural side: calyx lobes evident: the stylopodium low and flat (fig 2).

This species is decidedly distinct from any of the known species in this genus. Some of its characters suggest the genus *Phellopterus*, but the char-

acteristic caudex and the presence of the stylopodium leave scarcely any doubt that it is a *Cynomarathrum*.

Secured by MACBRIDE in the shale slides near the summits of the mountains bordering Bear canyon, in the Lemhi National Forest, July 31, 1911, no. 1502.

DODECATHEON PAUCIFLORUM **shoshonensis,** n. var.—Similar to the species in size, but the root system consisting of a short corm from which the fleshy-fibrous roots seem to detach at the end of the season, at which time there has formed laterally on the corm 1 or 2 elongated bulblike buds. These probably give rise to the next year's plants. The flowers are paler than in the species.

The material at hand is rather scanty and over-mature. Possibly ampler collections may show further differences. The specimens were secured by NELSON and MACBRIDE at Shoshone Falls, July 26, 1911, no. 1362.

Phacelia firmomarginata, n. sp.—Annual or possibly biennial,[2] divaricately branched from the base, with assurgent branched stems 1–2 dm. long: pubescence short, fuscous, obscurely glandular, with some small scattering hispid hairs which are most numerous on the calyx: leaves alternate, rather small, 1–4 cm. long, sessile or short-petioled, oblong in outline, pinnately cleft or parted into few ovate or obovate crenulate-toothed lobes: the ebracteate spikes dense even in fruit, 3–6 cm. long: calyx decidedly enlarged in fruit, apparently persistent, cleft to the base and only loosely inclosing mature capsule; sepals narrowly oblong-lanceolate, at maturity about 1 cm. long, reticulated by the veins which run from the stout mibrib to the greatly thickened firm hispid margins: corolla minute, pale or white, much shorter than the calyx, the rounded denticulate lobes about half as long as the short broad tube, the vertical folds obsolete; stamens and style well included: capsule ovoid, minutely hispid-pubescent, 3–4 cm. long, 4-seeded: seeds oblong, about 2 mm. long, brown, distinctly pitted.

Probably nearest *P. hispida*, from which it is quite distinct. It is a plant of the desert, being secured by MACBRIDE on dry hillsides near Twilight Gulch in Owyhee County, June 23, 1911, no. 979.

PHLOX LONGIFOLIA **filifolia,** n. var.—The woody caudex short, freely branched: the stems delicately filiform, 1–3 dm. long: leaves filiform, about 1 mm. broad, mostly 3–6 cm. long but often

[2] In full fruit June 23 and the root leaves largely wanting.

longer: bracts, pedicels, and calyx glandular-pubescent: corolla tube one-half longer to nearly twice as long as the calyx lobes.

The strongest character of the variety is its glandular inflorescence and its longer corolla tube. Represented by NELSON and MACBRIDE'S no. 1192 from Ketchum, July 19, 1911, found among the sagebrush on the river bottom lands.

Gilia Burleyana, n. sp.—Perennial from a completely lignified, rather large root, with a more or less branched caudex, producing few–many slender leafy suberect stems, 15–30 cm. high: pubescence scanty, soft and crisped, more abundant on stems and inflorescence than on the leaves: leaves alternate, small, numerous, entire, linear, 1-nerved, slightly thickened on the margins, mucronate-tipped, 1–4 cm. long: inflorescence capitate, or of 2 or more heads in a terminal congested corymb: flowers numerous, small and very crowded: calyx tube delicately scarious, twice as long as the greenish hirsute subulate mucronate lobes: corolla white, tubular, with more or less reflexed lobes half as long as the tube; tube less than 5 mm. long, slightly exceeding the calyx, obscurely pubescent within: anthers exserted; filaments inserted in the sinuses, shorter than the corolla lobes: style about equalling the stamens: ovules solitary in the cells, usually only one maturing and producing an inequilaterally distended capsule: seed large, oblong, slightly curved as is also the embryo, developing mucilage and spiracles when wetted.

This rather extraordinarily strong species falls into the section ELAPHOCERA Nutt. as arranged by Dr. BRAND in his recent monograph. Until now this section contained no perennials.

This species is named in honor of Mr. D. E. BURLEY, general passenger agent of the Oregon Short Line Railroad Company, whose cordial cooperation and intelligent interest in scientific work is so greatly appreciated. The type of the species is NELSON and MACBRIDE'S no. 1126, from loose white clay banks, a few miles from King Hill, Idaho, July 16, 1911.

Cryptanthe scoparia, n. sp.—About 15 cm. high, fastigiately branched from the base and upward, the erect branchlets broom-like in their compactness: pubescence of a few stiff hispid spreading hairs and a rather close layer of short white appressed ones: leaves linear, the hispid hairs from pustulate bases: racemes numerous, 3–6 cm. long at maturity: fruiting calyces numerous and rather crowded on the rachis: sepals very narrow, but thick, bluntly

subulate, 4–5 mm. long in fruit: corolla not seen: nutlets 4, about 2 mm. long, narrowly conical, attached their whole length by an open but narrow groove to a slender-subulate gynobase, the small areola at base scarcely forked, closely muricate with silvery-gray spinellae on a brown background.

Material in this genus is assigned with difficulty. Floral characters give but little clue. Aspect and the nutlets are the most reliable characters. Even these seem to vary much, but after making due allowance for this fact, the present specimens cannot be referred to *C. multicaulis* A. Nels., Bot. Gaz. **30**:194, nor to *C. grisea* Greene, Pitt. **5**:53, apparently the two nearest allies. Both of these differ essentially as to the nutlets.

The type is Nelson and Macbride's no. 1311, from sagebrush plains, near Minidoka, July 24, 1911.

Pentstemon confertus Dougl.—Perhaps in no group of *Pentstemon* does a tendency to vary with every change in the ecological conditions manifest itself so fully as in *P. confertus* and its allies. In this group there are three rather strongly marked species: *P. attenuatus*, *P. confertus*, and *P. procerus*, all by Douglas. In recent years several others have been added, some as species and some merely as varieties. How many of these should stand may not yet be said, but certainly not all of them. The undue multiplication of species might be held measurably in check if we could reach some agreement as to the relative importance of the characters ordinarily relied upon in describing these plants. The diagnostic characters mostly used are (1) pubescence in corolla throat and on the sterile filament, (2) shape and size of the corolla and the calyx lobes, (3) glandulosity of the inflorescence, (4) pubescence on the herbage, (5) color of the corolla. Now it is evident that if one phytographer considers one of these as of fundamental value in determining relationship, and another takes one of the other characters as basic, and a third still another, and so on, the number of species that may be described by the rearrangement of these characters becomes merely a problem in permutation. It seems, therefore, that one ought to place first those characters which are probably modified the least by reason of a change of environment, that is, those characters which are fundamentally concerned with the perpetuation of the species should stand first and the others should be serially arranged in the order in which they

relate themselves to this one great fact of reproduction. To illustrate: in this *Pentstemon* group the characters enumerated above may well stand in the order given, for is it not probable that those points of structure concerned with insect visitation come true generation after generation, while such as viscosity, pubescence, and color may change with every change of environment?

How close are the three species enumerated may be seen in the following facts: all have the sterile filament and the lower lip of the corolla more or less bearded; all have the flowers in verticils (two or more); all have calyx lobes more or less scarious-margined and mostly more or less lacerate. If one undertakes to state categorically their differences, about all one can say even of supposedly typical material is:

1. *P. attenuatus.*—Flowers yellow, rather large (20 mm. or more); inflorescence glandular and pubescent.

2. *P. confertus.*—Flowers yellow but small (less than 20 mm. long); inflorescence pubescent or puberulent but not glandular.

3. *P. procerus.*—Flowers not yellow (usually blue-purple), small (less than 20 mm. long); inflorescence neither pubescent nor glandular.

Of the three species, no. 2 seems most readily maintained as a pure and fixed species. The scores of variants may rather satisfactorily be grouped under 1 and 3. This being true, why not let the large-flowered forms, having the other floral characters in harmony, constitute the variety?

P. attenuatus **varians,** n. var., without reference to color or the presence or absence of pubescence or glandulosity.

Similarly let the small-flowered variants, having the other floral characters of *P. procerus*, become *P. procerus* **aberrans,** n. comb.

This varietal name was used by M. E. JONES as *P. confertus aberrans*, but the specimens to which the name was applied are clearly of the *P. procerus* group (see Proc. Cal. Acad. **2**:5–715).

I am fully aware that this disposition of this troublesome group means the wrecking of several pseudo-species, among which may be named *P. micranthus* Nutt., *P. Owenii* and *P. Rydbergii* A. Nels., *P. pseudoprocerus* Rydb., and a score (more or less) of Dr. GREENE'S species (see vol. I of *Leaflets*).

As excellent examples of *P. attenuatus varians*, I name MACBRIDE'S no. 974,

Twilight Gulch, Owyhee County, June 23, 1911, and his no. 1693, Pinehurst, Boise County, August 17, 1911.

Pentstemon laxus, n. sp.—Minutely puberulent on stems and foliage, the pedicels and calyx wholly glabrous: stems solitary or few, from a compact mass of thick fibrous roots, slender and weak, 5–8 dm. high: leaves 6–9 pairs, not much reduced above, lanceolate-linear, 5–10 cm. long: flowers in a crowded subcapitate terminal cluster on a peduncle 6–12 cm. long and naked but for 1 or 2 pair of linear approximate bracts; besides the terminal cluster there are rarely produced from the axils of the upper leaves a pair of small pedicellate clusters: calyx short, cleft to the base; its lobes broadly obovate, obtuse, slightly erose, scarious with greenish center especially toward the tip, only 2–3 mm. long or about one-fifth as long as the corolla: corolla a vivid blue, narrowly tubular and only slightly dilated upward, 2-lipped, but the lips short, the longer lower lip densely bearded with long yellow hair; the lobes all very short, suborbicular: stamens glabrous, shorter than the corolla: sterile filament shorter than the fertile, not dilated, blue at tip, tapering and flexed at the very apex, glabrous or with 1–7 deciduous hairs.

This is probably not a very strong species, but it seems fully as distinct from any *Pentstemon* previously discussed as any two of them are from each other. Further, if made merely a variety it would be difficult to say to which one to unite it.

It was found on slopes in rich sagebrush lands. NELSON and MACBRIDE, no. 1196, Ketchum, July 19, 1911.

PENTSTEMON LINARIOIDES **seorsus,** n. var.—Very similar to P. linarioides Gray (Bot. Mex. Bound. 112), from which it differs primarily as follows:

Larger in every way, the rootstock notably woody: calyx green and only half as long as the corolla; its lobes ovate, abruptly acute, thick and green at tip, slightly scarious below: corolla glabrous in the throat: the sterile filament longer than the fertile ones and densely pubescent with short yellow hairs for its whole length.

At first it seemed impossible that these specimens from southwestern Idaho should be referable to a species so long known only from southern Colorado, New Mexico, and Arizona, and the above characters led to their being desig-

nated as a new species, *P. seorsus*. On further reflection it seems better, however, to consider them as representing merely a variety.

Collected by MACBRIDE at Twilight Gulch, Owyhee County, in lava fields, June 22, 1911, no. 970.

PENTSTEMON ERIANTHERA **Whitedii,** n. comb.—*P. Whitedii* Piper, BOT. GAZ. **22**:490. 1901.

Mr. PIPER, in Contrib. Nat. Herb. **11**:500, reduces his species to a synonym of *P. erianthera* Pursh, but this was hardly justified. *P. erianthera Whitedii* is of different habit, producing several stems (instead of only 1 or 2) from a wood taproot; the stems are more slender; the leaves narrower and more numerous; the glandular-pubescence throughout is less pronounced; the sepals are lanceolate, acute (not acuminate); the corolla is light blue without any of the peculiar red found in typical *P. erianthera*. While the pubescence in the throat and on the sterile filament is of the same character, it is far less copious. For these reasons it seems that the northwest forms may well be carried as a variety of the typical Rocky Mountain *P. erianthera*.

NELSON and MACBRIDE'S no. 1421, secured at Mackay, on gravelly sagebrush slopes, July 30, 1911, is typical of the variety.

CASTILLEJA VISCIA Rydb.

The range of this excellent species is greatly extended by MACBRIDE'S no. 990 from Silver City, Owyhee County. While MACBRIDE'S plants are not quite typical, yet they help to a better understanding of the species. These are more densely glandular and lack the crimson or scarlet tips in bracts and corolla. The corolla is of the right proportions, but smaller.

Castilleja multisecta, n. sp.—Freely branched from a woody caudex, the ascending stems sparingly branched, 2–4 dm. high, including the long fruiting spike which is often more than one-third of the plant: pubescence inconspicuous, very softly lanate throughout: leaves 2–4 cm. long, numerous, pinnately parted into 5–7 narrowly linear lobes, the lateral ones sometimes again parted, the undivided base obcuneate and strongly 3-nerved: bracts resembling the leaves but the segments tipped with red, as are also the margins of the galea: calyx more deeply parted above than below, the primary lobes deeply toothed, the thin triangular teeth acute: corolla slender, about 3 cm. long; the galea being about one-third of this; the lower lip very short, saccate, its short broad truncate teeth with a central cusp: seeds beautifully honeycombed on the surface with shallow scarious cell walls.

In spite of the large number of species of *Castilleja* of somewhat similar aspects and with dissected leaves, I do not seem to be able to refer this to any near ally. The type number is NELSON and MACBRIDE'S 1261, secured on disintegrated granite slopes at Ketchum, Blaine County, Idaho, July 21, 1911.

MISCELLANEOUS SPECIES

Eriogonum loganum, n. sp.—Perennial with woody branched caudex, the current year's stems short, simple, leafy, densely white-lanate as are also the leaves, peduncles, and involucres, assurgent, 1 dm. or less long and terminating in a stout ascending scapelike peduncle 12–25 cm. high: leaves oblanceolate, mostly narrowly so, obtuse or subacute, very white and densely appressed lanate, 2–3 cm. long, on pedicels of about the same length: involucres tubular-campanulate, thin and scarious between the 5 or 6 nerves, 4–5 mm. long, many-flowered: perianth glabrous, pale (greenish-white), directly articulated to the capitate apex of the slightly exserted pedicels; perianth segments thin but with a stout rounded midrib raised on the inside, the outer and inner similar, oblong, obtuse, about 2 mm. long: achene glabrous, 3 mm. long, the ovoid-triangular body not longer than the tapering beak.

This description has been drawn from specimens supplied by CHARLES PIPER SMITH, of Logan, Utah, under no. 1704. It occurs on the dry bench lands or terraces near the college, and is in blossom late in June, with ripe achenes in July. These specimens have been referred to *E. ochrocephalum* Wats., but that species seems quite distinct from this.

LESQUERELLA LUNELLII **lutea,** n. var.—Much like the species, seemingly blossoming even the first year from seed, hence some specimens appear as annuals, some as biennials, and still others as perennials, with slender woody taproot: leaves narrowly oblanceolate: flowers yellow, a little larger than in the species.

This variety is probably only an ecological variation. Dr. LUNELL has now secured the species itself from several localities in Benson County, and these sustain the characters as originally given, including the purple blade of the petals. The variety he has secured in three other counties (Ward, McHenry, and Rolette), and it differs primarily in that the petals are yellow, as one expects them to be in this genus. It would no doubt have been more in harmony with our conception of the genus had the form with yellow petals been discovered and named first, the purple one becoming the variety.

Astragalus Batesii, n. sp.—Stems few to several, spreading from the summit of a slender woody taproot, only 1–4 cm. long, very leafy; leaves pinnate, 5–9 cm. long including the slender petiole; leaflets mostly 7–11, narrowly oblong, obtuse, strigose-canescent, greenish and becoming glabrate above: flowers in terminal, capitate, few–several-flowered racemes on very slender peduncles which in fruit equal or exceed the leaves; bracts lance-linear, silky, shorter than the silky calyx: calyx lobes linear, as long as the tube: corolla pale violet, 6–8 mm. long, exceeding the calyx, turning somewhat yellowish with age: pod strictly 1-celled, with straight keel except the tip, narrowly oblong, tapering to the acuminate or cuspidate tip, with short silky appressed pubescence, 12–15 mm. long, when mature lightly transverse rugose.

Rev. J. M. BATES, of Red Cloud, Neb., for many years a careful student of his local flora, contributes the fine specimens upon which this description is based. Having carefully studied the plant in the field and being familiar with the species of *Astragalus* of his range, he submitted this as probably different from any of the described species. In this opinion I must concur, and I therefore take this opportunity to dedicate the species to its discoverer. The species is most nearly allied to *A. lotiflorus* Hook. from which it is at once distinguished by its more appressed pubescence, its violet flowers, and its strictly 1-celled pod in which the dorsal suture is not at all impressed. The type is deposited in the Rocky Mountain Herbarium under the collector's no. 5501, Red Cloud, Neb., May 17 and May 23, 1911. A splendidly fruited specimen secured at the same place, June 9, 1909, in also deposited with the type.

Mertensia campanulata, n. sp.—Glabrous throughout, even to the calyx lobes: root thick and semi-fleshy, giving rise to few or solitary erect stems: stems moderately leafy, pale below: root leaves oblong, tapering to both ends, obtusish at apex, cuneate at base, the blade 8–12 cm. long, on petioles usually longer than the blade: stem leaves oblanceolate, tapering to a margined base, the middle ones the largest but these smaller than the root leaves, the uppermost very much reduced: panicle rather small and open, short-peduncled, 1–3 slender accessory peduncles from the uppermost leaves: calyx campanulate, about 5 mm. long, the broadly triangular obtusish lobes not more than one-fourth as long as the tube: corolla deep blue, beautifully veined with brown, 18–20 mm. long, tubular, the tube proper about half of it; the relatively long

throat but slightly dilated; the short lobes (3–4 mm.) abruptly reniformly expanded: anthers linear-oblong; filament inserted at the summit of the tube proper, as broad as the anther but only half as long, the two together as long as the throat: nutlets smooth or nearly so.

This seems to be an unusually strong species. Carelessly examined it might be referred to *M. ciliata*, but in reality it is closer to *M. Macdougallii* Rydb., of Arizona, from which it is clearly distinct and is equally distinct from *M. Leonardi* Rydb. Its calyx is distinctive in this genus.

Mr. C. N. Woods, supervisor of the Sawtooth National Forest, secured it "in moderately moist meadows" and sent in the ample specimens, at the same time calling attention to its salient characters. No. 325, Blaine County, Idaho, 1911.

University of Wyoming
Laramie, Wyoming

BENEFICIAL EFFECT OF CREATININE AND CREATINE ON GROWTH[1]

J. J. SKINNER

(WITH ONE FIGURE)

This paper embodies a series of experiments on the influence of creatinine and creatine on seedling wheat. These experiments were made in an endeavor to throw light on the action of organic manures in soils, and the influence of soil organic matter on productivity. Creatinine has been discovered as a soil constituent in this laboratory by Dr. E. C. SHOREY,[2] and an account of its occurrence and properties will be given elsewhere. This nitrogenous constituent occurs plentifully in animal products, wine, meat, etc., but has recently been found in these laboratories by Dr. M. X. SULLIVAN[3] to be a constituent part of many plants and seeds, and to occur in the medium in which plants have grown. The general methods for studying the effect of creatinine on plants in solution cultures is the same as that employed in connection with the harmful soil constituent, dihydroxystearic acid, previously reported in this journal.[4]

Effect of creatinine on growth

Two sets of cultures, composed of the fertilizer salts calcium acid phosphate, sodium nitrate, and potassium sulphate in varying proportions, used singly and in combinations of two and three, were prepared, the proportions varying in 10 per cent stages, thus making a total of 66 culture solutions according to the plan in the

[1] Published by permission of the Secretary of Agriculture, from the Laboratory of Soil Fertility Investigations.

[2] SHOREY, EDMUND C., The isolation of creatinine from soils. Jour. Amer. Chem. Soc. **34**:99. 1912.

[3] SULLIVAN, M. X., The origin of creatinine in soils. Jour. Amer. Chem. Soc. **33**:2035. 1911.

[4] SCHREINER, O., and SKINNER, J. J., Some effects of a harmful organic soil constituent. BOT. GAZ. **50**: 161. 1910; Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZ. **50**: 1. 1910.

papers cited. Young wheat seedlings were grown in this series of solutions from March 3 to March 15. To one set of the 66 cultures only the nutrient salts were added, to the second set 50 ppm. of creatinine were added to each culture. Every three days the solutions were changed and analyzed.

When the two sets of cultures had grown for several days, it was noticeable that the creatinine plants were better developed, having broader leaves and longer and well developed roots. This was more noticeable in some of the fertilizer mixtures than in others.

The total growth made in the 66 cultures of nutrient salts without creatinine, designated as normal cultures, was 166.7 grams as against 181.2 grams in the case of the 66 cultures with 50 ppm. of creatinine. Putting the normal at 100, the latter becomes 109, or an increase of 9 per cent as an average of the 66 cultures. As already mentioned, the effect was much more pronounced in certain fertilizer combinations, especially those containing no nitrates, or those low in nitrates. The effects of creatinine in these cultures will now be considered in detail.

Effect of creatinine on growth in cultures containing no nitrate

Table I gives the growth of two sets of cultures composed of mixtures of phosphate and potash, varying in 10 per cent stages,

TABLE I

SHOWING THE EFFECT OF CREATININE ON GROWTH IN CULTURES CONTAINING NO NITRATES

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURE IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	0	80	1.400	1.576
2	8	0	72	1.470	2.200
3	16	0	64	1.950	2.100
4	24	0	56	1.527	2.000
5	32	0	48	1.490	2.200
6	40	0	40	1.558	2.408
7	48	0	32	1.795	2.328
8	56	0	24	1.540	2.400
9	64	0	16	1.444	2.220
10	72	0	8	1.400	2.100
11	80	0	0	1.100	1.150

there being no nitrate in the solutions; the concentration was 80 ppm. of $P_2O_5+K_2O$ in each culture. To one set of cultures was added 50 ppm. of creatinine. In the fifth column are given the green weights of the cultures without creatinine, and in the last column are given the weights of the cultures with creatinine. It is apparent from these figures that the creatinine has caused a

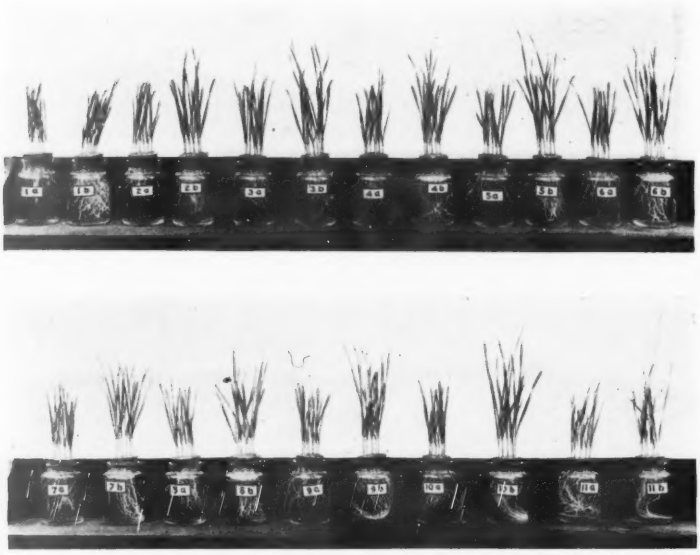


FIG. 1.—Wheat plants growing in culture solutions containing various proportions of potash and phosphate (with no nitrates) without (*a*) and with (*b*) creatinine.

considerable increase in growth. This is true in each of the 11 cultures. The total growth of the eleven cultures, without creatinine, was 16.674 grams against 22.682 grams for the cultures with creatinine. This is an increase of 36 per cent in the creatinine cultures.

The effect of creatinine in cultures with no nitrogen are shown in the plants in fig. 1. Cultures marked with the same number, for instance 1*a* and 1*b*, have similar fertilizer ratios. The cultures marked *a* have no creatinine, the numbers with the letter *b* have

50 ppm. of creatinine. As shown in the photograph, the plants in each culture containing creatinine, regardless of the proportion of potash and phosphate, is larger than the plants grown in a similar solution without the creatinine. The increased growth is noticeable in the roots as well as the tops. The tops in each case are broader and taller, the roots are larger and better branched.

Effect of creatinine in cultures containing 8 ppm. NH_3 as nitrate

Since creatinine was very beneficial in cultures containing no nitrate, it is interesting to observe its effect in cultures which contain a small amount of nitrate. Table II gives the result of the

TABLE II

SHOWING THE EFFECT OF CREATININE ON GROWTH IN CULTURE SOLUTIONS COMPOSED OF FERTILIZER MIXTURES, CONTAINING 8 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURE IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	8	72	1.820	2.190
2	8	8	64	2.470	3.100
3	16	8	56	2.748	3.250
4	24	8	48	2.907	3.420
5	32	8	40	2.670	2.450
6	40	8	32	2.928	3.258
7	48	8	24	2.526	3.340
8	56	8	16	2.600	3.000
9	64	8	8	2.048	2.359
10	72	8	0	1.354	1.750

effect of creatinine on growth in culture solutions composed of 8 ppm. of NH_3 as nitrate, and varying amounts of phosphate and potash, the total concentration of each solution being 80 ppm. of $P_2O_5+NH_3+K_2O$. By comparing the figures it is seen that the growth with creatinine, given in the last column, is larger than the growth without creatinine, given in the fifth column. The difference, however, is not nearly so large as in solutions containing no nitrate, presented in table I. The total green weight of the cultures composed of fertilizer mixtures containing 8 ppm. of nitrogen without creatinine was 24.071 grams against 28.117 grams in the cul-

tures with creatinine, an increase of 17 per cent. In the cultures with no nitrate creatinine produced an increase of 36 per cent.

Effect of creatinine in cultures with larger amounts of nitrate

It has been shown that creatinine was very beneficial in cultures which contained no nitrates. In a group of cultures, composed of mixtures of phosphate and potash in different proportions, creatinine increased the growth 36 per cent. It has also been pointed out that the beneficial effect of creatinine was not so great in cultures containing a small amount of nitrate. In a second group of cultures, composed of mixtures of potash, phosphate, and 8 ppm. of NH_3 as nitrate, creatinine increased the growth only 17 per cent.

In table III are given the results of growth in cultures with and without creatinine, composed of mixtures of phosphate, potash, and nitrogen having 16 ppm. NH_3 as nitrate. The green weights of the creatinine cultures given in the last column of the table are slightly larger than the normal cultures, as shown in the fifth column. The total green weight of the cultures without creatinine was 25.516 grams against 27.573 grams for the cultures with creatinine, an increase of 8 per cent.

TABLE III

SHOWING THE EFFECT OF CREATININE IN CULTURES CONTAINING 16 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatinine	With creatinine
1	0	16	64	2.200	2.570
2	8	16	56	3.200	3.720
3	16	16	48	3.500	3.500
4	24	16	40	3.097	3.702
5	32	16	32	3.250	3.250
6	40	16	24	3.228	3.300
7	48	16	16	2.975	3.240
8	56	16	8	2.626	2.551
9	64	16	0	1.440	1.740

In other cultures composed of the three fertilizer ingredients P_2O_5, NH_3, and K_2O, but containing 24 ppm. of NH_3 as nitrate, creatinine increased growth only 2 per cent. Its effect in cultures

composed of fertilizer mixtures having more than 24 ppm. of nitrate was uncertain; in some cases there was a slight increase in growth and in others there was a slight decrease, that is, the growth with these higher amounts of nitrate in the solution was practically the same in the normal and creatinine cultures.

Before discussing further the effect of creatinine, it will be necessary to recall the effect which nitrates have on the growth of plants in mixtures of the other two fertilizer ingredients potash and phosphate. In work previously published,[5] it was shown that the better growth occurred in the normal cultures when the three fertilizer elements P_2O_5, NH_3, and K_2O were present. It was best in mixtures which contained approximately equal amounts of NH_3 and K_2O and a small amount of P_2O_5 (about 16 ppm.). The growth in the cultures containing the three constituents was much greater than in the cultures containing only two constituents. This was especially marked when nitrogen was not in the composition. In illustration of this, the average growth of a number of cultures, composed of mixtures of phosphate and potash in amounts of 80 ppm. of $P_2O_5+K_2O$, was 1.000 gram against 3.155 grams as the average growth of cultures composed of mixtures of these two ingredients, with an addition of only 8 ppm. of NH_3 as nitrate, the total concentration of nutrients being the same. In a second experiment conducted in a similar manner, but at a later date, the average growth of the cultures, composed of mixtures of phosphate and potash, was 0.878 gram, and the average growth of cultures, in mixtures of the three ingredients, containing 8 ppm. of NH_3 as nitrate, was 2.107 grams.

In the present experiment the growth in the normal cultures composed of varying proportions of phosphate and potash, compared with the growth in mixtures of these two ingredients, with 8 ppm. of NH_3 as nitrate added, is given in table IV. By a close examination of the figures in this table, it is seen that the growth in the mixtures of phosphate and potash is smaller than in cultures composed of mixtures of the three ingredients, though containing

[5] SCHREINER, O., and SKINNER, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZ. **50**: 1. 1910. Some effects of a harmful organic soil constituent. Bull. 70, Bureau of Soils, U. S. Dept. Agric. 1910.

but 8 ppm. of NH_3. The average growth of the cultures without nitrogen is 1.516 grams against 2.407 grams with 8 ppm. of NH_3 in the fertilizer mixture. Putting the growth of the cultures without nitrogen at 100, the relative growth of the cultures with nitrogen becomes 159, or an increase of 59 per cent.

TABLE IV

SHOWING THE GROWTH OF CULTURES, COMPOSED OF FERTILIZER MIXTURES CONTAINING NO NITRATE, AND 8 PPM. OF NH_3 AS NITRATE, WITHOUT AND WITH CREATININE

No.	PPM. OF FERTILIZER INGREDIENTS IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS			
				Without creatinine		With creatinine	
	P_2O_5	NH_3	K_2O	No nitrate	8 ppm. NH_3	No nitrate	8 ppm. NH_3
1	0	0	80	1.400	.....	1.576	.....
2	0	8	72	.....	1.820	.....	2.190
3	8	0	72	1.470	.....	2.200	.....
4	8	8	64	.....	2.470	.....	3.100
5	16	0	64	1.950	.....	2.100	.....
6	16	8	56	.....	2.748	.....	3.250
7	24	0	56	1.527	.....	2.000	.....
8	24	8	48	.....	2.907	.....	3.420
9	32	0	48	1.490	.....	2.200	.....
10	32	8	40	.....	2.670	.....	2.450
11	40	0	40	1.558	.....	2.408	.....
12	40	8	32	.....	2.928	.....	3.258
13	48	0	32	1.795	.....	2.328	.....
14	48	8	24	.....	2.526	.....	3.340
15	56	0	24	1.540	.....	2.400	.....
16	56	8	16	.....	2.600	.....	3.000
17	64	0	16	1.444	.....	2.220	.....
18	64	8	8	.....	2.048	.....	2.359
19	72	0	8	1.400	.....	2.100	.....
20	72	8	0	.....	1.354	.....	1.750
21	80	0	0	1.100	.....	1.150	.....

With 50 ppm. of creatinine in the solution, the cultures containing no nitrogen produced better growth than the corresponding cultures without creatinine, as shown in the last two columns of table IV. The difference between the last two columns is not as marked in the creatinine set as in the corresponding columns for the normal set. The average growth of the creatinine cultures without nitrate is 2.062 grams against 2.812 grams for the cultures having 8 ppm. of NH_3 as nitrate in the fertilizer mixture. If the growth of the cultures without nitrate is put at 100, the growth with 8 ppm.

of NH_3 in the fertilizer mixture becomes 136, or an increase of only 36 per cent. In other words, in the absence of creatinine from the cultures, the nitrate (8 ppm.) caused an average increase of 59 per cent in the various cultures; in the presence of the creatinine (50 ppm.) the nitrate (8 ppm.) caused an average increase of only 36 per cent. It appears, therefore, that plants supplied with creatinine do not respond so markedly to added nitrate, thus seeming to indicate that the plant can utilize this nitrogenous compound for plant syntheses.

Effect of creatinine on absorption of fertilizer salts

The foregoing discussion has shown clearly the influence of creatinine on growth and its effect in cultures containing no nitrates. There remains to be discussed the effect of the creatinine on the removal of nutrients from the solution during the growth of the plant.

Mention has been made already of the fact that the concentration differences produced by the growth of the plants in the various cultures were determined by making an analysis for nitrates at the termination of every three-day change, and of the phosphates and potassium on a composite of the solutions from the four changes. It is thus possible to compare the results obtained under the so-called normal conditions without the creatinine and under the conditions where 50 ppm. of creatinine were present in the solution.

The sum total of P_2O_5, NH_3, and K_2O removed from solution by the growing plants in the cultures containing all three of these constituents was 1684 milligrams under the normal conditions, and 1584 milligrams in the creatinine set. The figures show the total of plant nutrients to be slightly less in the creatinine set, although the green weight in this set was 9 per cent greater than in the normal set. The examination of the results for the three constituents separately as given below, shows that the phosphate and potash were slightly greater than normal, as is demanded by the larger growth, whereas the nitrate is considerably less than in the normal set.

Phosphate.—The amount of phosphate stated as P_2O_5 removed from the total number of solutions during the experiment was 364 milligrams for the normal cultures and 383 milligrams for the cul-

tures containing creatinine, a difference of 19 milligrams in favor of the creatinine cultures.

Potassium.—The amount of potash stated as K_2O removed by the plants in the total number of cultures was 760 milligrams in the case of the normal cultures and 778 milligrams for the cultures with creatinine. As with the phosphate, the creatinine cultures removed a little more potash than the normal cultures, there being a difference of 18 milligrams in favor of the creatinine set.

Nitrogen.—The total amount of nitrogen stated as NH_3 removed from the total number of solutions during the course of the experiment was 560 milligrams for the normal cultures and 423 milligrams for the creatinine cultures. The creatinine cultures though making a larger growth used 137 milligrams less nitrate.

Effect of creatine on growth

Creatine is closely related chemically to creatinine, the latter being the anhydride of creatine. Both probably occur in soils, manures, and green crops, a discussion of which is given in the two other papers referred to. Experiments in nutrient cultures with creatine have been conducted similar to those with creatinine.

The plants grew from April 22 to May 4. After the plants had grown for several days, it was apparent that the effect of creatine was very similar to that of creatinine. The leaves were broader, and further developed than those of the normal culture. The roots were longer and better branched. The plants growing in cultures with creatine, which contained phosphate and potash but no nitrate, were a great deal larger than similar cultures without creatine. Like the creatinine, when small amounts of nitrate were in the fertilizer mixture, the beneficial effect of creatine was not so marked, and in the presence of larger amounts of nitrate creatine had no additional effects.

The total green weight of 66 cultures containing the fertilizer salts only, that is the normal set, was 174.4 grams, against 186.8 grams for the 66 cultures containing 50 ppm. of creatine in addition to the fertilizer salts. This is an increase for the creatine cultures of 8 per cent over the normal cultures.

Table V shows the effect of creatine on growth in a number of

cultures containing varying amounts of phosphate and potash, but no nitrates, the amount of total fertilizer ingredient in each culture being 80 ppm. By an examination of the table it is apparent that the growth of each of the creatine cultures given in the last column is considerably larger than the growth of the cultures without creatine given in the fifth column. The total green weight of the cultures without creatine was 16.2 grams against 23.3 grams for the cultures with creatine, an increase of 44 per cent.

TABLE V

SHOWING THE EFFECT OF CREATINE ON GROWTH IN CULTURES CONTAINING NO NITRATE

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatine	With creatine
1.....	0	0	80	1.329	1.709
2.....	8	0	72	1.420	1.948
3.....	16	0	64	1.558	2.130
4.....	24	0	56	1.579	2.370
5.....	32	0	48	1.528	2.470
6.....	40	0	40	1.500	2.400
7.....	48	0	32	1.670	2.270
8.....	56	0	24	1.628	2.420
9.....	64	0	16	1.600	2.450
10.....	72	0	8	1.428	2.070
11.....	80	0	0	0.978	1.090

In table VI are given the green weights of plants grown in cultures with and without creatine, containing 8 ppm. of NH_3 as nitrate and varying amounts of P_2O_5 and K_2O, the total constituents being 80 ppm. of $P_2O_5+NH_3+K_2O$. These figures show that the creatine cultures given in the last column are somewhat larger than the cultures without creatine given in the fifth column, but the difference is not nearly so large as in the cultures containing no nitrate given in table V. The total growth of the cultures without creatine was 26.4 grams against 29.4 grams for the cultures with creatine, an increase of only 11 per cent in favor of the creatine cultures. There was a difference of 44 per cent in favor of the creatine cultures in the case of the solution which contained no nitrate.

The growth in the cultures which contained varying amounts of phosphate and potash and 16 ppm. of nitrate was only 3 per cent greater with than without creatine. In solutions containing 24 ppm. of nitrate the increased growth with creatine was 6 per cent, and in solutions containing 32 ppm. nitrate the increased growth 4 per cent. In solutions containing higher amounts of nitrate the creatine had no additional effect. Thus it appears that the effect of creatine in replacing the effect of nitrate in producing growth is very similar to that of creatinine.

TABLE VI

SHOWING THE EFFECT OF CREATINE ON GROWTH IN CULTURES CONTAINING 8 PPM. OF NH_3 AS NITRATE

No.	PPM. OF FERTILIZER INGREDIENT IN CULTURE SOLUTION			GREEN WEIGHT OF CULTURES IN GRAMS	
	P_2O_5	NH_3	K_2O	Without creatine	With creatine
1	0	8	72	2.299	2.459
2	8	8	64	2.940	3.200
3	16	8	56	2.700	3.350
4	24	8	48	2.920	3.400
5	32	8	40	3.050	3.070
6	40	8	32	3.150	3.309
7	48	8	24	3.220	3.350
8	56	8	16	2.500	2.854
9	64	8	8	2.222	2.800
10	72	8	0	1.400	1.600

It is also interesting to note the effect of creatine on the removal of salts by the plants and the similarity between the action of creatine and creatinine in this respect. It will be remembered that in the creatinine cultures the removal of phosphate and potash was slightly greater in the creatinine cultures than the normal cultures, but a great deal less nitrate disappeared from solution in the creatinine than in the normal cultures.

In the creatine experiments the removal of total P_2O_5, NH_3, and K_2O by plants in the normal cultures was 1978.3 milligrams, against 1854.5 milligrams for the creatine cultures. The normal cultures removed 471.0 milligrams of P_2O_5 and the creatine cultures 474.4 milligrams. In the case of potash the normal cultures

removed 769.4 milligrams of K_2O against 767.4 milligrams for the creatine cultures. The removal of both phosphate and potash was practically the same in the normal and creatine cultures. The disappearance of nitrate was much less in the creatine than in the normal cultures. The normal cultures removed 737.7 milligrams against 612.7 milligrams for the creatine cultures, a difference of 125 milligrams.

The influence of the creatine in regard to the removal of P_2O_5, NH_3, and K_2O is very similar to that shown by creatinine, and it again appears that this substance as well as the creatinine can replace nitrates in its effect on plant growth.

Bureau of Soils, U.S. Department of Agriculture
Washington, D.C.

BRIEFER ARTICLES

A NOTE ON THE GENERATIONS OF POLYSIPHONIA[1]

(WITH ONE FIGURE)

YAMANOUCHI[2] concludes from his cytological work on *Polysiphonia violacea* that "there is an alternation of a sexual plant (gametophyte) and an asexual plant (sporophyte) in the life history of *Polysiphonia*, the cystocarp being included as an early part of the sporophytic phase." He found that on the cystocarpic plants there was an occasional abnormality "in the form of a cell resembling a monospore, but having the same cell lineage as the tetraspore mother cell." He traced the development of these cells and found that although cleavage furrows appeared, the nucleus rarely entered a mitosis and the cell never divided. He makes note of the fact that LOTSY has found tetraspores on the same plants with sexual organs in *Chylocladia kaliformis* and that DAVIS has found the same condition in *Spermatothamnion Turneri*, *Ceramium rubrum*, and *Callithamnion Baileyi*. He suggests that possibly the structures reported as tetraspores are really monospores and are developed with a suppression of reduction phenomena, or that the sexual organs are developed apogamously.

LEWIS[3] has attempted an experimental test of the truth of YAMANOUCHI'S conclusion. He says: "Cytological observations on *Polysiphonia* by YAMANOUCHI, on *Griffithsia* by myself, and on *Delesseria* by SVEDELIUS render it probable that in these genera at least, and presumably in all Florideae in which tetraspores and sexual organs are borne on separate individuals, there exists an alternation of sexual and asexual plants, the carpospores giving rise on germination to asexual, and the tetraspores to sexual individuals." The results that he obtained by growing plants from the spores of *Polysiphonia violacea*, *Griffithsia Borneliana*, and *Dasya elegans* are consistent with the above theory, no carpospores having been found to produce sexual individuals, and no tetraspores to produce asexual individuals. Both the cytological and the experimental evidence would thus seem to unite in indicating that

[1] Contributions from the Puget Sound Marine Station, no. 2.

[2] YAMANOUCHI, S., The life history of *Polysiphonia*. BOT. GAZ. **42**:401–449. 1906.

[3] LEWIS, I. F., Alternation of generations in certain Florideae. BOT. GAZ. **53**:236–242. 1912.

there is an alternation of generations in at least *Polysiphonia violacea*, and to offer at least some foundation for the belief that it is general among the red algae.

In 1911 Professor T. C. FRYE found in *Polysiphonia* material, collected at the Puget Sound Marine Station in 1910, some specimens showing both carpospores and tetraspores on the same individual. This observation was made in the course of laboratory work with a class and no material was kept. He suggested to the senior author of this note that the subject be investigated further at the Puget Sound Marine Station. The junior author examined the *Polysiphonia* material that was brought into the laboratory at the station during the session of 1911. In one lot of material she found the same condition to which Professor FRYE had referred. The material was collected in the lower littoral zone on the rocky shore of Turn Island, near Friday Harbor, Washington. It has been identified by Professor W. A. SETCHELL of the University of California as *Pterosiphonia bipinnata* and by Dr. SHIGÉO YAMANOUCHI of the University of Chicago as *Polysiphonia* sp.

FIG. 1.—Camera lucida drawing of a portion of a *Polysiphonia* (?), showing on the same individual both tetraspores and a cystocarp with a carpospore.

The fact that the mother cells had gone to the point of complete division into tetraspores in the material examined indicates that the tetraspores were not abortive, and the fact that carpospores were seen issuing from cystocarpic plants that bore also perfect tetraspores indicates that the cystocarps were not abortive. We have thus an individual that is both sexual and asexual, which is inconsistent with there always being in this species an alternation of a sexual individual and an asexual.

Professor T. C. FRYE and the senior author of this note are now at work on the cytology of specimens of this species with a view to determining the sporophytic or gametophytic nature of this generation by means of mitotic studies.—GEORGE B. RIGG and ANNIE D. DALGITY.

CURRENT LITERATURE

BOOK REVIEWS

Forest physiography[1]

This volume, intended primarily for the use of foresters, will be of very great value to ecologists, even to those working upon problems which are unrelated to forests. Its field of usefulness extends farther still, for it is the first work in which the much-scattered literature dealing with the physiography of various parts of the United States has been summarized and systematized. It will thus be frequently consulted by geologists, geographers, economists, and travelers. The ecologist as a rule must work out for himself the physiographic processes which are in immediate operation in his field of study. The value of Professor BOWMAN's work will be found to lie principally along two lines: in the clearing up of the physiographic history of the region, and in comparison of the field of study with other parts of its physiographic region and with other regions.

The book comprises two parts. Part I is entitled "The soil," and is a summary of the present knowledge of that subject as it pertains to forest growth. This section is included because the influence of the physiographic processes upon forests is exerted largely through the formation, modification, and destruction of soils. It seems to the present writer that a better plan would have been to expand this section into a separate work, since the two parts of the book are essentially independent. The topics treated are as follows: importance, origin, and diversity of soils; physical features; water supply; temperature; chemical features; humus and nitrogen supply; soils of arid regions; soil classification.

In part II the physiography of the United States is considered by regions, each subdivision having "an essential uniformity or unity of geologic and physiographic conditions," and therefore a uniform topographic expression in the main. The sequence is from west to east. An introductory chapter discusses physiographic, climatic, and forest regions. In consideration of climate, full recognition is given to the combined effect of the various factors upon plant distribution, and yet MERRIAM's "life zones" are accepted, although they are based upon temperature alone.

The chapters devoted to the various physiographic regions are largely descriptive of the present topography, with only such geologic details as are necessary to explain it. As the author remarks in the preface, the forester

[1] BOWMAN, ISAIAH, Forest physiography. pp. xxii+759. *pls. 6. figs. 292.* New York: John Wiley & Son, 1911.

is concerned with the relief of a region rather than with its geologic history. At the same time, the historical treatment is entirely adequate to satisfy the needs of an ecologist, and abundant references to the literature are given for the benefit of any who wish more detailed information. To illustrate the mode of treatment, the section devoted to the Adirondack Mountains may be cited. The subdivisions are as follows: geologic structure, topography and drainage, glacial effects, climate and forests.

The notes upon the forests which are appended to most of the sections are the least satisfactory portions of the work, being so brief and general as to be almost useless, and in one case at least inaccurate. The conifer forest of the southern Appalachian summits is referred to in three places. On p. 122 it is correctly described as "spruce and balsam." On p. 125 we read of the "spruce and hemlock forests on the summits of the Pisgah and other ranges in western North Carolina, where boreal conditions exist." The hemlock in these mountains is found principally in deep ravines in the lower hardwood forest belt, and rarely attains to the lower margin of the spruce-balsam forest. On p. 614 occurs the statement that "on the higher summits of the Great Smoky, Pisgah, and Balsam Mountains are a few thousand acres of black spruce," with no mention of the balsam, which is the more important of the two. On the same page, the author places the hemlock where it rightly belongs, in "shaded ravines and on the better watered northern or northwestern slopes between 3000 and 5000 feet."

The book is adequately illustrated and has valuable physiographic and geologic maps. Its great weight is to be regretted, in a volume which one would wish to carry upon his travels.—WILLIAM S. COOPER.

A Yosemite flora

Professor and Mrs. H. M. HALL of the University of California are pioneers in the production of a local flora or handbook of one of our great natural playgrounds. Scores and scores of other local floras have been produced, but these have been as a rule mere check lists, and in all cases were intended to meet a local need. In this *Flora of the Yosemite*[2] we have a handbook that will find its largest use among strangers to the region. It is hardly necessary to call attention to the small size of this National Park as compared with the size of the great state of California, nor to the great size of the Park *botanically* considered. Within its 1024 square miles there are probably more kinds of soil and climate than can be found in any equal area in the world. This varied topography and climate have supplied the 955 species included in the flora. The grasses, sedges, and rushes are not included, but the authors conservatively estimate that these would swell the number to 1200, a number probably as great as that of an entire state in the prairie region.

[2] HALL, HARVEY MONROE and CARLOTTA CASE, A Yosemite flora. San Francisco: Paul Elder & Co. $2.16.

The book possesses practically every feature that will contribute to its usefulness: an introduction to the Park itself; a chapter on the organography of the plant for those who have not had a course in botany; simple but complete keys; plain concise descriptions with a minimum of technical terms; interesting notes on habitat, habit, distribution, etc; 11 beautiful halftone plates in brown, and 174 instructive figures; a glossary and a complete index. This little manual of nearly 300 pages is significant in many ways. It indicates an increasing interest in technically correct science simply and clearly expressed. It emphasizes the fact that systematic botany should be developed for the *use* of the people, not to *impress* them with the futility of trying to fathom the mysteries of recent nomenclatural practices. It shows that the breeze is beginning to blow steadily from the ocean, littered with the wreckage of families, genera, and species, to the solid shores on which an *Astragalus* is an *Astragalus* and not a *Tium;* a *gentian* is a *gentian* and not an *Anthopogon;* and a *pine* is a *pine* and not an *apine.*

When a thing is so well done it seems almost ungenerous to mention matters which represent merely differences of opinion, but would it not have been well to have included the grasses, sedges, and rushes for the sake of completeness? Botanists would have valued this feature even if the descriptions had been very much curtailed. Attention may also be called to the seeming ultra-conservatism of the authors in the matters of the adoption of recent names for old, well known species. To a beginner, one technical name is as good as another, and no useful purpose is served by retaining a name that properly belongs in another range, even though that name has long been used in ours.

The publishers have done their work well. The binding is limp leather, the paper excellent in quality, and the pages are trimmed close, so that the little volume feels good in the hand and will no doubt find its way into the pockets of many of the visitors to the Yosemite Park.—AVEN NELSON.

NOTES FOR STUDENTS

Current taxonomic literature.—L. R. ABRAMS (Muhlenbergia **8**: 26–44. 1912) gives a synoptical revision of the genus *Monardella,* as represented in southern California, and adds 4 new species, and 3 varieties.—O. AMES (Torreya **12**: 11–13. 1912) has published a new *Habenaria* (*H. Brittonae*) from Cuba.—J. C. ARTHUR (Mycologia **4**: 49–65. 1912) records the results of continued studies on the "Cultures of Uredineae in 1911."—O. BECCARI (Webbia **3**: 131–165. 1910) under the title "Palmae australasiche nuove o poco note" has published several new species of palms and proposes a new genus (*Pritchardiopsis*) of this family from New Caledonia.—A. BRAND (Rep. Sp. Nov. **10**: 280, 281. 1912) characterizes a new genus (*Namation*) of the Scrophulariaceae based on the Mexican plant *Nama glandulosum* Peter. The same author (*ibid.* 281) proposes the name *Andropus carnosus* for the plant hitherto doubt-

fully referred to the genus *Conanthus*.—N. L. Britton (Bull. Torr. Bot. Club **39**:1–14. 1912) under the title "Studies of West Indian plants IV" places on record important data and describes 20 new species of flowering plants.—The same author (Torreya **12**:30–32. 1912) adds a new species to the recently monographed genus *Hamelia*, namely *H. scabrida* from Jamaica.—N. L. Britton and J. N. Rose (*ibid.* 13–16) record 7 hitherto undescribed species of cacti from Cuba.—E. Chiovenda (Ann. Bot. **10**:25–29. 1912) under the title "Intorno a due nuovi generi di piante appartenenti alla famiglia delle Malpighiaceae" proposes two genera, namely *Tetraspis* and *Eriocaucantus*.—A. Cogniaux (Rep. Sp. Nov. **10**:343, 344. 1912) describes a new species of *Epidendrum* (*E. Rojasii*) from Paraguay.—L. Diels (Leafl. Phil. Bot. **4**:1161–1167. 1911) gives a synopsis of the Philippine Menispermaceae, recognizing 14 genera; the synopsis is based on a monograph of the group in the *Pflanzenreich* by the same author.—K. Domin (Rep. Sp. Nov. **10**:57–61, 117–120. 1911) describes several species of flowering plants from Australia and proposes a new genus (*Notochloe*) of the Gramineae.—A. D. E. Elmer (Leafl. Phil. Bot. **4**:1171–1474. 1911–1912) in continuation of his work on the Philippine flora has described upward of 150 new species of flowering plants.—A. Engler (Bot. Jahrb. **48**:224–336. 1912) in collaboration with several specialists has issued "Beiträge zur Flora von Afrika XL." About 120 species new to science are published, belonging mostly to the Solanaceae, Polygonaceae, and Umbelliferae. Four new genera of the Umbelliferae are proposed, namely *Afrosison*, *Marlothiella*, *Volkensiella*, and *Frommia*.—F. Fedde (Rep. Sp. Nov. **10**:311–315, 364, 365, 379, 380, 417–419. 1912), has published new species and varieties of *Corydalis* from North America.—M. L. Fernald and K. M. Wiegand (Rhodora **14**:35, 36. 1912) record a new variety of *Juncus* (*J. balticus* var. *melanogenus*) from Quebec.—C. N. Forbes (Occ. Papers Bern. Pau. Bish. Mus. Ethl. and Nat. Hist. **5**:1–12. 1912) under the title "New Hawaiian plants III" has published 4 new species of flowering plants.—E. L. Greene (Leafl. Bot. Obs. and Crit. **2**:165–228. 1912) has described about 100 new species of North American flowering plants mostly referred to *Apocynum* and *Erigeron*.—D. Griffiths (Rep. Mo. Bot. Gard. **22**:25–36. *pls. 1–17*. 1911) in a fourth article on *Opuntia* has described and illustrated 10 new species from southwestern United States and Mexico.—W. B. Grove (Journ. Bot. **50**:9–18, 44–55. *pls. 515, 516*. 1912) in an article entitled "New or noteworthy Fungi, part IV" includes the description of a new genus (*Cryptostictella*) found on leaves of *Tilia europea* at Studley Castle, England.—The same author (*ibid.* 89–92) has proposed the generic name *Diplosphaerella*, to include the species which have 16 spores in the ascus; the genus is based on *Mycosphaerella polyspora* Johans.—E. Hackel (Rep. Sp. Nov. **10**:165–174. 1911) under the title "Gramineae novae VIII" describes several new species of grasses including 9 from Mexico and South America.—E. Hassler (*ibid.*, 344–348. 1912) has published new species and varieties in the Rutaceae, Simarubaceae, and Scrophulariaceae from Paraguay.

—A. A. HELLER (Muhlenbergia **7**:125–132. 1912) describes and figures a new species of *Ivesia* (*I. halophila*) from the Ruby Mountains, Nevada; and (*ibid.* **8**:21–24. *pl. 4*) records a new *Apocynum* (*A. cinereum*) from the same state.—G. HIERONYMUS (Rep. Sp. Nov. **10**:41–53, 97–116. 1911) has published 19 new species of *Selaginella* from the Philippine Islands.—P. B. KENNEDY (Muhlenbergia **7**:133–136. 1912) describes a new willow (*Salix caespitosa*) from Mt. Rose, Nevada.—F. D. KERN (Torreya **11**:211–214. 1911) records 2 new species of *Uromyces* from the Central and Southern States.—F. KRÄNZLIN (K. Sv. Vet. Akad. Handl. **46**: no. 10. 1–105. *pls. 1–13.* 1911) under the title "Beiträge zur Orchideenflora Südamerikas" has published 78 new species of orchids, mostly from Brazil. The descriptions are supplemented by illustrations bringing out the more salient floral characters.—G. KÜKENTHAL (Leafl. Phil. Bot. **4**:1169–1170. 1911) records a new *Carex* (*C. palawanensis*) from the Philippine Islands.—H. LÉVEILLÉ (Rep. Sp. Nov. **10**:431–444. 1912) has published several new species of flowering plants from China and the Sandwich Islands and includes a new genus (*Esquirolia*) of the Oleaceae from China.—I. M. LEWIS (Mycologia **4**:66–71. *pls. 58–61.* 1912) describes and illustrates a new black knot disease (*Bagniesiella Diantherae*) found on *Dianthera americana* at Austin, Tex.—J. LUNELL (Am. Mid. Nat. **2**:169–177, 185–188, 194, 195. 1912) describes new species and varieties in *Laciniaria*, *Toxicodendron*, and *Gutierrezia*.—T. H. MACBRIDE (Mycologia **4**:84–86. *pl. 62.* 1912) describes and illustrates a new *Geaster* (*G. juniperinus*) from Iowa.—T. MAKINO (Bot. Mag. Tokyo **25**:251–258. *pl. 7.* 1911) under the title of "Observations on the Flora of Japan" describes and illustrates a new genus (*Mitrastemon*) which represents a monotypic family (Mitrastemonaceae) of parasitic plants from the temperate regions of Japan, and regarded by the author as constituting an independent series (Mitrastemonales) most closely allied to the Aristolochiales.—U. MARTELLI (Webbia **3**:5–35. 1910) presents a synoptical revision of the genus *Freycinetia* of the Philippine Islands, recognizing 35 species of which 9 are indicated as new.—W. R. MAXON (Bull. Torr. Bot. Club **39**:23–28. 1912) records the results of a study of the genus *Phanerophlebia* and gives a key to the 7 recognized North American species.—W. MOESER (Rep. Sp. Nov. **10**:310, 311. 1912) characterizes a new genus (*Pseudobotrys*) of the Icacinaceae from New Guinea.—W. A. MURRILL (Mycologia **4**:72–83. 1912) in a fifth article on the "Agaricaceae of tropical North America" treats 13 genera and describes new species in *Mycena*, *Pluteolus*, *Conocybe*, *Naucoria*, *Cortinarius*, *Inocybe*, and *Hebeloma*. The same author (*ibid.* 91–100) gives a list of the Polyporaceae and Boletaceae collected on a recent tour of the Pacific Coast region; the article includes 8 new species of the former family and 4 of the latter.—J. A. NIEUWLAND (Am. Mid. Nat. **2**:178–185. 1912) describes two new species and four varieties of flowering plants, and (*ibid.* 201–247) in an article entitled "Our amphibious Persicarias" discusses several of the aquatic or semiaquatic smartweeds and proposes 2 additional species in the group.—J. M. GREENMAN.

Geotropism.—RITTER[3] applies the rotation method of PICCARD[4] for determining the distribution of geotropic sensitiveness in various grass seedlings. RITTER states that it is through the application of this brilliant conception alone that the distribution of geotropic sensitiveness has been settled in some cases.[5] In *Avena sativa*, *Hordeum vulgare*, and *Phalaris canariensis*, a short tip zone of the coleoptile is very much more sensitive than the basal region, which shows some geotropic sensitiveness. In *Avena* the very sensitive zone is 3 mm. long, and in *Hordeum* and *Phalaris* 4–5 mm. In *Setaria italica* all regions of the coleoptile are equally sensitive, while in *Sorghum vulgare* the tip region shows slightly greater sensitiveness. Since the main curving is in the epicotyl, a conduction of the stimulus to that region from the coleoptile must occur. The distribution of the motile starch in all these organs corresponds closely with the distribution of geotropic sensitiveness, so that RITTER considers the work confirmatory of, or at least not antagonistic to, the statolith starch theory.

In a study of the geotropism of rhizoids carried out in HABERLANDT'S laboratory, BISCHOFF[6] comes to the following conclusions: The rhizoids of the growing gemmae of *Marchantia polymorpha* and *Lunularia cruciata* are, contrary to the conclusion of WEINERT, positively geotropic, and those of the thalli show the same character with lower sensitiveness. BISCHOFF asserts that the lack of motile starch in these rhizoids does not necessarily argue against the statolith theory, for other motile bodies may take its place. The rhizoids of ferns are ageotropic. The main rhizoid of mosses (*Bryum capillare*, *B. argenteum*, and *Leptobryum pyriforme*) is positively geotropic in light, while the protonemata and side rhizoids are ageotropic. In the mosses statolith starch is found in the main rhizoid.

JOST and STOPPEL[7] have established the interesting fact that under high centrifugal force of sufficient duration the roots of *Lupinus* give the negative geotropic response instead of the positive. For negative response 16 gravities or more are needed for decapitated roots, and 70 gravities or more for intact ones. This lines geotropic response up with OLTMANN'S findings for heliotropic response; one and the same organ responds either positively or negatively, depending upon the strength of the stimulus. Parallel with heliotropism a

---

[3] RITTER, HERMAN VON GUTTENBERG, Über die Verteilung der geotropischen Empfindlichkeit in der Koleoptile von Gramineen. Jahrb. Wiss. Bot. **50**: 289–327. *fig. 1*. 1912.

[4] PFEFFER, W., Physiology. English ed. **3**: 418–419. 1905.

[5] See review of DARWIN in BOT. GAZ. **46**: 387. 1908; also review of HABERLANDT in BOT. GAZ. **47**: 482–483. 1909.

[6] BISCHOFF, HANS, Untersuchungen über den Geotropismus der Rhizoiden. Beih. Bot. Centralbl. **28**: 94–133. 1912.

[7] JOST, L., and STOPPEL, R., Studien über Geotropismus. II. Die Veränderung der geotropischen Reaktion durch Schlenderkraft. Zeitsch. Bot. **4**: 207–229. 1912.

medium intensity of the stimulus produces no reaction; also the positive curving occurs in the zone of most rapid growth, while the negative takes place in the region of greater maturity. The *quantity of stimulus law* already established for heliotropism and geotropism[8] is confirmed by this work. The quantity of stimulus necessary for a negative response is about 1000 times that necessary for a positive response.

JOST[9] takes up the several positive arguments that have been offered in favor of the starch statolith theory, and with some partisanship shows their shortcomings. He observes that the negative argument is often used; that while many facts do not aid in substantiating the theory they at least do not disprove it. This statement holds, he asserts, because the theory itself has experienced a gradual process of adaption to the demands of newly established facts, which makes the theory of 1909 quite a different thing from that of 1900. In its earlier form the starch must actually fall on the *Plasmahaut* and lie there for some time to induce the reaction, while in the later form movement of the starch without geo-perception is explained by lack of irritability of the plasma, and geo-perception without movement of starch is explained by saying that actual displacement of the starch is not necessary for perception.

The author has studied the response of the root on the Piccard centrifuge and the effect of the removal or injury of various regions of the root tip on geo-perception and geo-response. The results on the Piccard centrifuge agree with those of HABERLANDT,[10] though the author gives them a different interpretation, which he believes accords better with all the facts known. Any injury that leaves the root tip attached or removes 0.5–0.75 mm. gives a wound effect that hinders geo-response for some hours. Removal of 1 mm. or more of the tip hinders geo-response for many days. JOST believes removal of 1 mm. or more of the tip affects the response in three ways: by wound shock, by removing a highly sensitive geo-perceptive region, by removing a region of great tonic significance in rendering other regions sensitive. His main evidence for the tonic effect of the tip 1 mm. is the fact that on the Piccard centrifuge the tip must extend over the point at least 1.5 mm. to give a reaction in favor of the tip, showing considerable sensitiveness in the growth zone; while removal of only 1 mm. of the tip renders the growth zone ineffective. The author believes that NĚMEC's conclusion that statolith starch is necessary in the tip for geo-perception lacks evidence, and that such a conclusion was drawn because NĚMEC failed to recognize the important tonic effect of the tip 1 mm. JOST believes that the meristem of the tip, along with the cap region immediately bordering on it on the one hand and the growth region on the other, are the regions of the maximum sensibility, while other regions may perceive but give

[8] See review of BLAAUW in BOT. GAZ. **49**: 238. 1910.

[9] JOST, L., Studien über Geotropismus. I. Die Verteilung der geotropischen Sensibilität in der Wurzelspitze. Zeitsch. Bot. **4**: 161–205. 1912.

[10] See review in BOT. GAZ. **47**: 482. 1912.

no results unless the tip is present. The meristem in *Lupinus*, the form used, is starch free, consequently this interpretation which seems to agree well with all facts observed is opposed to the starch statolith theory.—WILLIAM CROCKER.

Gummosis.—SORAUER,[11] in two extensive papers, discusses gum-flow in the cherry and related phenomena in some other trees. He concludes that the tendency to gummy degeneration is latent in the cherry tree, and that stimuli such as frost and wounds only accentuate a natural tendency. Individual cells in the pith and bast, which in perfectly normal twigs of various trees show swelling of the walls and discoloration and degeneration of the contents, exhibit the primary evidences of the tendency to gummosis. Through variations in growth that may be regarded as normal, such as unusual breadth of the medullary rays, or through variations in nutrition affecting turgor, or through wounds, effects of frost, etc., the tension relations between pith and wood, and between wood and bark, are frequently greatly altered, resulting in release of pressure at certain points. At these points, islands of parenchymatic cells are regularly formed, among and in place of the normal prosenchymatic cells. This is a common phenomenon in many trees, without gummosis following; but in the cherry such islands of cells are the usual foci of gummy degeneration. They are particularly numerous in the wood formed by late fall growth; consequently different parts of the same branch or tree vary enormously in the tendency to gummosis.

Cells having the tendency to gummosis are deficient in starch, thin-walled, with heavy deposits of tannin and phloroglucin; in a word, they are cells which fail to mature. The cause of degeneration may be regarded as an excess of enzymes; degeneration in the individual cell starts in the cell contents, and extends to the secondary membrane, which swells and furnishes the chief material for the gum. As the gummosis extends to adjacent cells the order is of course reversed, the intercellular substance being first attacked, the cell contents last.

The bulk of these papers is devoted to a minute description of the histology and microchemical reactions of a great quantity of material illustrating various aspects of the gummosis problem. In addition to various species and varieties of *Prunus*, the following species are studied: *Corylus avellana*, *Pinus Laricio*, *P. silvestris*, *Fagus silvatica*, *Fraxinus excelsior*, *F. Ornus*, *Syringa vulgaris*, *Cytisus Laburnum*, *Tilia* sp., *Ampelopsis* sp., *Platanus* sp., and the pear. Scant attention is given to the work of previous investigators. These papers are of great value for the abundance of detailed observations, but the logic of the deductions is at times difficult to follow.

---

[11] SORAUER, PAUL, Untersuchungen über Gummifluss und Frostwirkungen bei Kirschbäumen. Landwirtsch. Jahrb. **39**: 259–297. *pls. 5.* 1910; and **41**: 131–162. *pls. 2.* 1911.

BUTLER[12] rejects the earlier view of BEIJERINCK and RANT, that gummosis is due to a cytase which, unable to attack the wall of a living cell does so as soon as the cell is injured from any cause. He also rejects RUHLAND'S view that the gum is an oxidation product of carbohydrates and that gummosis is caused by admission of air through wounds. BUTLER considers that "gummosis is due to hydrolysis of the walls of the embryonic wood cells, which develop into a susceptible tissue." The form of development of a spot of gummosis shows, however, that it is correlated with release of pressure of the cortical tissues. Gummosis does not occur unless the cambium is growing actively and there is an abundant supply of water available to the roots; when these two conditions are present gummosis may develop "autogenously" or be induced by any sort of injury that stimulates growth of the cambium. Contrary to previous investigators, BUTLER states that starch and other cell contents play no part in gum formation. "Gummosis of *Prunus* and gummosis of *Citrus* are indistinguishable maladies." Both squamosis and exanthema are considered to be forms of gummosis. An excellent bibliography is appended.—HAVEN METCALF.

Root habits of desert plants.—In studying the roots of plants growing near the Desert Laboratory, Tucson, Ariz., CANNON[13] has made a rather detailed investigation of more than 60 species, including winter and summer annuals as well as various types of perennials. Three general types of root systems are recognized, namely, a generalized system with both tap and lateral roots well developed, a specialized type with the tap root the chief feature, and a second specialized type in which the laterals, placed near the surface of the ground, are especially well developed. The cacti are almost the sole representatives of the last type, and represent a specialization of a xerophytic form capable of absorbing a water supply from rains which penetrate a few centimeters only. This type seems necessarily limited to plants with very considerable water-storage capacity. A further specialization in the roots of most cacti is to be seen in the development of an anchoring and an absorbing system.

Plants having prominent tap roots include comparatively few species. They are mostly perennial in habit and limited in their distribution to areas with considerable depth of soil. In contrast, the generalized system is characteristic of the majority of both the perennial and annual species. It facilitates distribution because of its plasticity, and because its representatives are found in widely varying situations. It is to be regarded as the least xerophilous of

---

[12] BUTLER, ORMOND, A study on gummosis of *Prunus* and *Citrus*, with observations on squamosis and exanthema of the *Citrus*. Ann. Botany **25**: 107–153. *pls. 4*. 1911.

[13] CANNON, W A., The root habits of desert plants. Carnegie Institution of Washington. Publ. No. 131. pp. 96. *pls. 23*. 1911.

the three systems, and hence includes almost all the annual plants. Few of these annuals penetrate the soil deeper than 20 cm., and most of the lateral branches are less than half this distance from the surface. Competition is evident between the various members of the generalized type, and also between them and those of the first specialized class. The best development of root systems is found in the summer annuals, due to more favorable vegetative conditions, and particularly to more favorable soil temperature during that portion of the year.

The details of root development in the various species are illustrated by many photographs and drawings, while the detailed descriptions contain many interesting facts concerning the different plants.—GEO. D. FULLER.

Chromatophores and chondriosomes.—FORENBACHER[14] has made a study of the origin of chloroplasts and leucoplasts in the stem and root of *Tradescantia virginica*, the object of which is to show the origin of these structures from chondriosomes (filamentous mitochondria). Beginning with the fully formed chloroplasts of the stem cortex and leaves and proceeding toward the tip, he finds a complete gradation between the fully formed chloroplasts and the chondriosomes. The intermediate forms present themselves as dumbbell and granular structures which gradually pass over into the chromatophores. Similar gradations are found between the chondriosomes (mitochondria) of the root tip and the leucoplasts. This work thus confirms the results of PENSA and LEWITSKY and those of GUILLIERMOND on the origin of the chloroplasts from mitochondria (chondriosomes).

Some doubt is justified of the efficiency of the methods employed for demonstrating the chondriosomes of plant cells. MEVES, for example, found these structures in the tapetal cells of *Nymphaea*, but not in the spore mother cells, in which, however, by suitable methods they may be shown to be very numerous. The reason was the small power of penetration of the fixing fluid, which did not reach the deeper tissues before the mitochondria had undergone change or disappeared. In eliminating acetic acid wholly from his fixing fluid, FORENBACHER has diminished its already slight power of penetration. His figures are not convincing, for the structures labeled as chondriosomes do not conform in shape or number to the usual condition in rapidly dividing cells of higher plants. It is quite possible that his young chloroplastids do not belong to the category of mitochondria (chondriosomes) at all.—R. R. BENSLEY.

Vascular anatomy of Salicales.—Miss HOLDEN[15] has investigated the position of Salicales on the basis of the vascular anatomy of the North American

[14] FORENBACHER, AUREL, Die Chondriosomen als Chromatophorenbildner. Ber. Deutsch. Bot. Gesells. **29**:648–660. *pl. 25*. 1911.

[15] HOLDEN, RUTH, Reduction and reversion in the North American Salicales. Ann. Botany **26**:165–173. *pls. 20, 21*. 1912.

representatives. In the ENGLER arrangement, based on floral characters, they are one of the three most primitive groups of the Archichlamydeae. Most of the eastern representatives of the group have uniseriate rays and "terminal" parenchyma ("only at the end of the annual ring") in the stem cylinder, but in the conservative regions multiseriate rays and vasicentric parenchyma are found. This latter combination is found also in the stem cylinders of certain western forms. The conclusion from these facts is that multiseriate rays and vasicentric parenchyma represent the primitive condition of the group, and that their present simple structure is due to a reduction from a more complex structure. This means that, according to the testimony of vascular anatomy, the Salicales should be transferred from a very low position to a relatively high one among the Archichlamydeae.—J. M. C.

The fruit of Compositae.—LAVIALLE[16] has begun the publication of a volume of observations on the development of the wall of the akene of the Compositae, a complex of testa and pericarp. The first chapter and part of the second have appeared in the *Annales* as cited. Since 298 species, representing 65 genera, have been studied, the number of observations are very great. Just what the value of them will be is also obvious. In the account of the "actual state of knowledge of the structure of the fruit of Compositae," the actual state of knowledge of the author is very apparent. The citations are few, and apparently no contributions in English were available.—J. M. C.

A new Cordaites.—Miss BENSON[17] has described a new species of *Cordaites* from a fairly well preserved specimen obtained from the coal mines at Shore, England. It is compared with related species, and the intimation is given that along with *C. Wedekindi* Felix it may represent a new genus, whose seeds are already suspected to be those of a *Mitrospermum* closely associated with it in the deposit. The whole leaf is said to have "a markedly xerophilous character."—J. M. C.

---

[16] LAVIALLE, P., Recherches sur le développement de l'ovaire en fruit chez les Composées. Ann. Sci. Nat. Bot. IX. **15**: 39–64. 1912.

[17] BENSON, MARGARET, *Cordaites Felicis*, sp. nov., a cordaitean leaf from the Lower Coal Measures of England. Ann. Botany **26**: 201–207. *pl. 22. fig. 1.* 1912.

Morphology of Gymnosperms

By JOHN M. COULTER AND CHARLES J. CHAMBERLAIN

IN 1901, Coulter and Chamberlain published their "Morphology of Gymnosperms," which brought together in organized form the results of research up to that time. The book was based partly on original work by the authors and partly on material from the reports of other investigators, and it at once took its place as the standard work on the subject.

The immense increase of knowledge in this field during the last decade has made necessary a thorough revision of the book. This is now presented to the scientific world in the belief that it will be no less useful than the first edition. Each of the seven great groups is presented in detail, and a final chapter discusses the problem of phylogeny and points out the evolutionary tendency. The presentation is so systematic that no index is necessary. The illustrations are numerous and to a great extent original. The book is intended not only for the use of investigators but for advanced students in the morphology of gymnosperms.

470 pages, 402 illustrations, 8vo, cloth. Postpaid $4.22

The University of Chicago Press
Chicago · · · Illinois

Esterbrook Steel Pens

250 Styles

A surprising amount of care is used in making Esterbrook Pens, but the superiority of the finished product more than warrants it.

The standard of the world.

Fine, medium and broad points. At all stationers.

Write for illustrated booklet.

The Esterbrook Steel Pen Mfg. Co.
95 John Street, New York
Works, Camden, N. J.

THERE ARE TWO REASONS

Why We Send Our

Daus Improved Tip Top Duplicator

ON TEN DAYS' FREE TRIAL.

FIRST—It proves OUR confidence in the machine.

SECOND—By personal use, YOU can positively tell before buying, whether it meets your approval or not.

Each machine contains a continuous roll of our new "DAUSCO" OILED PARCHMENT BACK duplicating surface which can be used over and over again. Five different colors can be duplicated at the same time. Cleanliness and simplicity of operation and legibility of copies unequalled by any other duplicating process.

100 Copies from Pen-Written and 50 Copies from Typewritten original

Complete Duplicator, cap size, (prints 8½ x 13 in.) **$5.00**

Price $7.50 less special discount of 33⅓ per cent net

FELIX E. DAUS DUPLICATOR CO. Daus Bldg., 111 John St., NEW YORK

The Life History of Polysiphonia Violacea

By SHIGEO YAMANOUCHI.

34 pages, 12 plates, 8vo, paper, net $1.00, postpaid $1.03

Various authors have published accounts of investigations on the red algae, but the true life-history of the group has never been given. This paper presents first the results of the author's studies of the mitosis in germinating tetraspores and carpospores, and in the vegetative cells of mature plants; then comes an account of spermatogenesis, formation of procarp, fertilization, and development of cystocarp; tetraspore formation is next considered, followed by a description of certain abnormalities; finally there is a discussion of the cytological phenomena and alternation of generations.

ADDRESS DEPT. P

Chicago **THE UNIVERSITY OF CHICAGO PRESS** Illinois

ORDERS and inquiries from individual buyers of books in quantities, schools, and libraries solicited. The most prompt and complete shipment of orders, at lowest prices for all parts of the country—the best service in the United States.

Ask us to send you our

STANDARD LIBRARY CATALOGUE NO. 10

and

THE MONTHLY BULLETIN

of the

Latest and Best Selling Books

THE BAKER & TAYLOR COMPANY

Publishers and dealers in the books of all publishers

33-37 East 17th Street **NEW YORK CITY** Union Square North